CALIFORNIA FISH AND GAME

"CONSERVATION OF WILDLIFE THROUGH EDUCATION"

VOLUME 54 JULY 1968 NUMBER 3

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ERRATUM

Tomlinson, Patrick K. Mortality, growth, and yield per recruit for Pismo clams. 54(2) : 100–107, 1968.

The formula near the bottom of page 101 should be

$$M = -4 \log_e(N_t/N_o)$$

and the formula at the lower left corner of Table 1, page 102 should read

$$M = -4 \log_e(N_t/N_{t-.25}).$$

RETIREMENT

J. B. PHILLIPS

The Department lost one of its most esteemed employees when Julie Phillips retired on May 1, 1968. The extent of the regard in which he was held is well demonstrated by the action of the State Assembly Rules Committee which adopted this resolution prepared by the Hon. Alan G. Pattee, assemblyman of the thirty-fourth district in which Julie lived:

> WHEREAS, Mr. Julius B. Phillips, Marine Biologist of the Department of Fish and Game, will retire on May 1, 1968, after a career of dedicated service to the people of California; and
>
> WHEREAS, Julius B. Phillips entered state service on August 6, 1928, as a deputy, and was appointed a fishery biologist in 1929 at Pacific Grove, a research zoologist in 1931, an assistant aquatic biologist in 1945, and an associate marine biologist in 1947; and
>
> WHEREAS, During the past four decades he has continued to serve the people of Pacific Grove, Monterey County, and the entire state in these capacities, and in others, with great distinction, dedication and integrity; and
>
> WHEREAS, His scientific studies and publications on the important marine resources of this state, most notably those on rockfish and sardine, have earned him a worldwide reputation and brought great credit to the State of California; and
>
> WHEREAS, Over this period of four decades his friendly counsel, unassuming attitude, quiet manner, and devotion to duty have earned him the respect of all those who came in contact with him; and
>
> WHEREAS, Julius B. Phillips richly deserves the pleasures of retirement by his significant contribution to the conservation of the marine resources of this state; now, therefore, be it
>
> *Resolved by the Assembly Rules Committee*, That the Members commend Julius B. Phillips on the occasion of his retirement and express their sincere thanks for his important contributions to the welfare of the marine resources of the state; and be it further
>
> *Resolved*, That the Chief Clerk of the Assembly transmit a suitably prepared copy of this resolution to Julius B. Phillips.

There is little we in the Department can add to this tribute save to express our own feeling of loss at his departure and to wish him and his wife a long and happy retirement.—*P. M. Roedel.*

Calif. Fish and Game, 54(3) : 133–155. 1968.

THE EMBRYOLOGY OF THE ENGLISH SOLE, *PAROPHRYS VETULUS*[1]

JAMES J. ORSI
Delta Fish and Wildlife Protection Study
California Department of Fish and Game

Mature fish were artificially spawned and the eggs incubated at 10.6 C ± 0.4 C, and the larvae were raised in 2-liter beakers or quart jars at the same temperature.

Egg samples were preserved and sectioned to study changes not visible in living material. Photomicrographs were taken.

The unfertilized eggs average 0.98 mm in diameter. They are transparent and spherical, lacking oil globules and pigment. They have numerous small oil droplets and the surface of the egg membrane is pierced by many small pores and is thrown into fine ridges.

Fertilized eggs average 0.99 mm in diameter. They have a very small perivitelline space, a thickened fertilization membrane, and float with the animal pole down. Early cleavages conform to the typical teleost pattern. They begin 2 hours after fertilization and continue at 1-hour intervals. No segmentation cavity exists because the periblast adheres to the lower surface of the blastomeres. Gastrulation begins at 25 hours and produces a large subgerminal cavity. Blastopore closure is at 48–49 hours, when the eye vesicles, olfactory sacs, neural cord, notochord, Kupffer's vesicle, and 11 somites have formed.

An unusual caudal vesicle arises at this time and becomes located behind Kupffer's vesicle. Its history and significance in *P. vetulus* is discussed.

Hatching begins at 98 hours and continues for 10 hours more. Newly hatched larvae are 2.85 mm TL, have unpigmented eyes, and float with the yolk sac up. Eye pigmentation is completed between 6 and 9 days. The yolk sac is absorbed at 9 or 10 days, and an average length of 4.6 mm is reached between 9 and 12 days. In the absence of food, the last surviving larvae die at 14 days.

INTRODUCTION

Few detailed embryologies of teleost fishes have been written. In addition, sometimes omissions and involved discussions make it difficult for the fisheries biologist to obtain a clear picture of teleost development. Nelsen (1953) and Balinsky (1965) describe the embryologies of all vertebrate groups, but their treatment of teleosts is sketchy. Therefore, I decided to trace the development of all the organs of a teleost fish to hatching and to describe the appearance of the larvae until the yolk was absorbed.

I chose the English sole, *Parophrys vetulus*, because it was easily obtained and spawned and, aside from the pelagic adaptations of its eggs, appeared to be relatively unspecialized embryologically. A brief description of this species' embryology has been published (Budd, 1940).

[1] Submitted for publication August 1967. Revision of Master of Science Thesis, University of Washington, College of Fisheries, 1965.

METHODS

Ripe English soles were otter trawled from Puget Sound, Washington, from January to March of 1964 and 1965 by the College of Fisheries vessel *M/V Commando*. The fish were held in an aquarium until spawned (usually 1 to 3 days).

The eggs from two or three females were spawned into a quart jar of sea water and fertilized immediately by sperm from one or two males. After 5 minutes, the contents of the jar were decanted into an incubator (a glass funnel or quart jar). Approximately 200 eggs were placed in the jars and 1,000 in the funnel. The latter, with a mouth diameter of 1 foot and a capacity of 5.9 liters, was filled with 2.2 liters of water and floated in a 200-gallon tank. A plastic ring with a piece of plankton netting sewed over it was fitted inside the funnel well below the surface of the water to prevent the loss of living eggs when the water was changed and to catch dead eggs when they sank. Water was removed through a plastic hose connected to the neck of the funnel and replaced by pouring, which also provided some aeration.

The water in the quart jars was neither changed nor aerated. This had no apparent ill effect on the eggs.

A constant circulation of water in the 200-gallon tank kept the temperature at 10.6C ± 0.4C during incubation.

The larvae were raised in 2-liter beakers or quart jars floating in the tank with the eggs, at the same temperature, and in semi or total darkness. There were approximately 50 larvae in each jar and 100 in each beaker. No attempts were made to insure their survival other than giving them an initial supply of clean water.

Three hundred and fifty living, unfertilized eggs and 100 living fertilized eggs from 14 females of varying sizes were measured with a filar micrometer. Newly hatched larvae were also measured with a filar micrometer. For older larvae, an ocular micrometer on a dissecting microscope was used. Twenty-five larvae were measured at each stage, unless otherwise noted in the text.

I preserved 10 to 20 eggs hourly until the formation of the germ ring. After this, I took samples at 2- or 3-hour intervals until hatching.

Stockard's solution was used as a preservative, since it caused much less distortion and shrinkage than the usual 5% formalin. I removed the yolk and egg membranes with microneedles, embedded the germ tissues in paraplast, sectioned them at 5μ, and stained them in haematoxylin and eosin.

EARLY DEVELOPMENT

Unfertilized Eggs

The unfertilized eggs of the English sole are transparent, spherical, lack oil globules and pigment, and average 0.98 mm (0.91–1.04) in diameter. When first extruded, they float at the surface but if not fertilized within 15 to 30 minutes, usually sink to the bottom.

The eggs faintly resemble a ball of yarn because of numerous low ridges traversing their surfaces. These ridges vary considerably in appearance and concentration. In general, the ridges, which are folds of the zona radiata or egg membrane, are short and straight or slightly

curved and run at right angles to the egg equator. In some eggs, the ridges appear cross-hatched, while in others they are nearly absent.

The egg membrane is pierced by many fine pores, arranged in a regular, even pattern. In the cytoplasm beneath the egg membrane are many small clear oil droplets of varying sizes, linked into roughly circular, anastomosing chains. Just below these chains are a few scattered droplets, twice as large as the biggest ones above them.

Even in the unfertilized egg, the cytoplasm can be seen as a thin layer ensheathing the yolk, and a small blastodisc with a micropyle already has formed at the animal pole. The micropyle is a shallow depression 0.032 mm in diameter, and only slightly deeper than the egg membrane is thick.

Fertilized Eggs

Fertilized ova average 0.99 mm (0.93–1.05) in diameter. These measurements are greater than those from California fish (Budd, 1940), which averaged 0.9 mm (0.89–0.93).

The eggs float with the animal pole, the region of the forming blastodisc, downwards. After fertilization, no changes take place in the surface ridges or in the oil droplets, but a perivitelline space appears, and the egg membrane thickens and becomes the fertilization membrane.

The perivitelline space of the English sole is very small. It is widest near the edges of the blastodisc, becomes gradually thinner toward the egg equator (Figure 2A), and virtually disappears at the vegetal pole.

Budd (1940) attributes the formation of the perivitelline space to the compression of the yolk by the forming blastodisc. The present theory (Kusa, 1956; Yamamoto, 1962) states that the cortical alveoli (spheres 10–40μ in size, located in the cytoplasm) break down on fertilization and release a hydrophilic colloid (a polysaccharide). The high osmotic pressure of this colloid causes the uptake of water, usually from the cytoplasm (more rarely from the environment), and this separates the fertilization membrane from the cytoplasm and fills the perivitelline space. If the cytoplasm contributes the water, it shrinks, but the elevation of the fertilization membrane increases the egg diameter. I do not know the source of the perivitelline fluid in *P. vetulus*, since I never observed an egg at the moment of fertilization. Such observation is necessary, because any loss in cytoplasm volume would be slight and difficult to measure.

The egg membrane thickens when some of the material expelled from the cortical alveoli fuses with it (Rothschild, 1958). This causes the water hardening of the egg. The resulting fertilization membrane in the English sole is three times as thick as the original. It is divided into two parts: a thin outer layer, the former zona radiata, and a thicker inner one.

Early Cleavage

The yellow-tinted blastodisc slowly increases in size from its pre-fertilization condition without visible streaming of cytoplasm. The whitish yolk underlying the blastodisc changes in shape as the cytoplasm accumulates above it. A saucer-shaped depression appears in it, becomes progressively larger, and then fluctuates in size.

At the onset of cleavage, 2 hours after fertilization, the blastodisc has increased from one-twentieth to one-sixth the diameter of the egg and

the yolk depression has disappeared. The blastodisc's sides are generally smooth and flow gradually into the protoplasm surrounding the egg. The first cleavage furrow begins in the center of the blastodisc's top. Next, a secondary furrow arises on the bottom of the blastodisc and forces the forming blastomeres to arch upwards. This secondary furrow diminishes and disappears as the primary one cuts through; it does no actual cleaving. The blastomeres do not separate completely. A strand of protoplasm unites them at their bases and more protoplasm remains around them (Figure 2A). This forms the periblast.

As cleavage progresses, the sides of the blastomeres become more distinct and rounded. This process continues after the furrow has been completed. I used the rounding up of the blastomeres as a criterion for the completion of this and subsequent stages. At a temperature of 10.9C the two-cell stage requires 20 minutes for completion.

The second cleavage furrow begins 3 hours after fertilization. Placed at a right angle to its predecessor, it starts in the center of both cells simultaneously and proceeds outwards, inwards, and downwards. It reaches the first cleavage furrow before it touches the outer edges of the blastomeres. A secondary furrow also exists in this stage.

The four blastomeres are flat on their inner sides (those touching each other) and round on the outer edges. They are elongated in the direction of the second cleavage furrow and are undercut so that they jut out a bit over the periblast, which swells underneath the margins of the cells. It takes 14 minutes to complete this stage at 10.9C.

The eight-cell stage begins 4 hours after fertilization and is complete 10 minutes later. Four furrows arise on the outer edges of each blastomere at right angles to the second cleavage furrow and cut inwards. The elongation of the blastomeres, noted in the four-cell stage, persists in this stage as an elongation of the blastoderm and small oil droplets can still be seen over and around the blastomeres. They are apparently carried to the blastodisc by the migrating cytoplasm.

The fourth cleavage begins 5 hours after fertilization. The furrows run at right angles to the third cleavage furrows and hence are parallel to and on either side of the second furrow. Cleavage is not simultaneous in all cells. Approximately 8 minutes is required to form the 16-cell blastoderm. This blastoderm is still slightly elongated, although different blastoderms vary considerably in shape. Some 16-cell blastoderms are well rounded up or even square.

In another hour, the fifth cleavage forms the two-layered 32-cell blastoderm. The 4 central cells of the 16-cell group cleave in the horizontal rather than the vertical plane, creating a core of eight cells, around which the remaining 24 cells are grouped in a single layer. Sometimes, the corner cells of the 16-cell blastoderm divide meridionally and the others split parallel to the sides of the blastoderm. Usually, however, the cleavage planes are irregular and difficult to determine.

Periblast

Focusing through the blastomeres, the periblast emerges as a dark, irregular ring under and around the peripheral cells of the blastoderm. It cannot be seen under the central cells in living eggs; however, in sections the periblast continues under the central cells as an extremely thin strip, which explains its invisibility in living material.

The periblast adheres to the bottoms of the blastomeres and the marginal blastoderm cells are continuous with it.

In time, the central, subblastodermic periblast thickens and nuclei appear on it. Nuclei also appear in the peripheral, extrablastodermic periblast (Figure 2F). They are derived, at about 10 hours after fertilization, from the breakdown of the marginal cells of the blastodermal cap. At this time, the edges of the cap are broken and irregular. Small tongues of cells stretch into the periblast and occasional isolated cells or cell clusters are adrift in it. Sections reveal that the marginal cells have lost their lower boundaries.

The marginal cells contribute nuclei to the periblast until shortly before gastrulation begins; at this time the connection between the marginal cells and the periblast is severed. If the connection persisted, cells attempting to invaginate over the blastoderm lip would either be blocked by the periblast or would carry it along with them.

Initially, the elongated periblastic nuclei are strewn haphazardly about. Later, they form as many as 6 rings around the blastodermal cap (Figure 2F). These nuclei become extremely large, rivalling the blastomeres in size. Their function is to metabolize the yolk to provide material for the growth of the embryo (Balinsky, 1965).

Blastodermal Cap

Continued cell multiplication transforms the 32-cell blastoderm into the many celled and layered blastodermal cap. Although the number of cells greatly increases, the size of the cap does not. It reaches a maximum height of approximately 10 cells at 15 hours and resembles a dome resting on the yolk. Its cells are polygonal, with the exception of the roofing layer of apithelial cells which have begun to flatten out (Figure 1A). After 15 hours, the cap hollows out in the center and becomes concave on the yolk side (Figure 2B). It pulls away from the fertilization membrane and spreads a short way down over the yolk surface. The blastoderm center is reduced to half its original thickness by 25 hours and the epithelial layer is complete. Now the germ ring forms and invagination begins.

Subgerminal Cavity

Up to this point, no space exists between the blastomeres and the periblast. The periblast clings to the blastomeres even when the blastoderm's undersurface becomes concave. Shortly before invagination, small scattered spaces gape open between the two tissues and they become very loosely connected. The invaginating tongue of cells thrusts under the blastodermal cap and pushes the periblast in front of it away from the blastoderm. In a short time, periblast and blastoderm are completely separated over the entire central region of the blastoderm, even where the invaginating layers have not penetrated. The late segmentation or subgerminal cavity so formed is shallow and ends at the invaginated cell plate, to which the periblast firmly adheres.

Gastrulation

Gastrulation transforms the small, single-layered blastoderm into a larger, multi-layered embryo. This is accomplished by two simultaneous

processes: invagination and epiboly. Invagination moves cells from the exterior to the interior of the blastoderm to form the multi-layered embryo. By epiboly, the blastoderm overgrows the yolk. It enables the embryo to reach a greater size than it could if restricted to the area around the animal pole.

In preparation for gastrulation, the edge of the blastoderm becomes thicker than the central region. This ring of cells is called the *rand wulst* (Figure 1A). Gastrulation begins when blastoderm cells roll over the blastoderm edge and grow inward from the inner tip of the *rand wulst*. The starting point for this ingrowth is the dorsal lip of the blastopore (the future posterior end of the embryo). The previously mentioned hollowing of the blastoderm leaves one half thicker than the other. The midpoint of this half becomes the dorsal lip. Invagination then occurs all around the circumference of the blastoderm, creating a zone of invagination termed the germ ring (Figure 2C). Looking at the blastoderm from below during early gastrulation, the inner edge of the newly formed germ ring is visible around the blastoderm (Figure 2F).

The dorsal lip of the blastopore is the main as well as the initial point of invagination. From it, the overwhelming bulk of the embryo is derived. A second gateway for ingrowing cells is the blastopore's ventral lip (Figure 2C), which furnishes a small amount of material to the tail at blastopore closure. Invagination at other points produces only the germ ring.

The invagination at the blastopore's dorsal lip becomes a broad pointed plate of cells that moves inward between the periblast and the blastoderm, following the curve of the blastoderm over the yolk. This plate is one cell thick at its tip and two cells thick at its base. The long axes of these cells are parallel to their direction of growth and are at right angles to the axes of the blastomeres above them.

As the invaginated cells migrate toward the future anterior end of the embryo, the germ ring moves in the opposite direction and spreads down the yolk, covering it with a single-celled sheet of ectoderm.

The broad plate of invaginated material and the thickened ectoderm above it are termed the embryonic shield (Figure 2C); around it are the thinned-out extra-embryonic areas. Endoderm and mesoderm arise from the invaginated cells; ectoderm and neural ectoderm arise from the nonmigrating cells.

The Early Embryo

At approximately 41 hours, the notochord becomes distinct from the anlage of the head down to the germ ring, where it somewhat broadens. Epiboly has now covered three-quarters of the yolk. Slightly later, the head thickens and suggestions of the future eyes can be made out as triangular swellings or vesicles lateral to the brain. Two hours before blastopore closure, the olfactory sacs appear anterior to the eyes and lateral to the forebrain. Kupffer's vesicle makes its first appearance at 46 hours as a small, round, clear space at the posterior end of the embryo near the closing blastopore. Somites start to form near the center of the embryo at 44 hours. They are open laterally to the mesoderm, which splays out on either side of the notochord. When the blastopore

closes, approximately 11 somites have been blocked out. The embryonic shield looks like a double concave lens when viewed from above. It is wide at the head, narrow in the midbody region, and spreads out again toward the germ ring. Some periblast nuclei, round rather than elliptically shaped, float over the yolk of the closing blastophore. Two tissue sheaths invest the yolk: the periblast, and above it either the embryonic shield or the extra-embryonic ectoderm.

Summing up, at blastopore closure the eye vesicles are lateral swellings, between them lies the brain, and anterior to them are the olfactory sacs. The notochord runs from the hindbrain to the germ ring, extending past the 11 somites that have formed up to Kupffer's vesicle.

ORGANS OF MESODERMAL ORIGIN

Notochord

The notochord first becomes visible in living embryos at 41 hours, when it separates from the mesoderm lying next to it; however, for some time before this, it is visible in sections as a bulge under the neural ectoderm.

Anteriorly, the notochord dips toward the ventral surface of the embryo and ends under what will become the anterior end of the hindbrain (Figure 3D). Posteriorly, it widens and vanishes in the region of the germ ring. Shortly after, it ends above Kupffer's vesicle, where it becomes confluent with the neural ectoderm. When the undifferentiated caudal mass arises from the fusion of the blastopore lips, the notochord merges into it.

Notochordal cells, polygonal in the earliest stages, adopt a flattened disc form by the time of blastopore closure. This gives the notochord a similarity to a stack of coins (Figure 3D). Before vacuolation of the notochord begins, they assume a tapered disc shape.

As the tail grows out after the blastopore closes, the notochord forms just behind it, passing Kupffer's vesicle and outstripping the somites. It reaches the tail tip at 74 hours.

Just in back of its tapered anterior end, vacuolation commences at about the same time the notochord reaches the tip of the tail (Figure 3C). The cells are very compressed, the nuclei lie on one side or other of the notochord, and the cytoplasm of the cells stretches almost to the vanishing point in crossing the notochord. Spaces appear within the cells, becoming larger and spreading down the notochord. Eventually, the center of the notochord is hollowed out, except for strands of cytoplasm criss-crossing it (Figure 1C). The nuclei and remaining cytoplasm are flattened around the periphery, where they form a sheath. At hatching, only the posterior end of the notochord is still solid.

Somites

The invaginated mesoderm spreads out as flat wings on either side of the notochord. Starting in the center of the embryo at 44 hours, somites form in both directions. They reach close to the auditory sacs and the tail tip by the time of hatching.

Originally, the somites are flat plates wider than they are deep. Gradually, the mesodermal wings pull in toward the midline, first in the anterior part of the embryo and then in the posterior part. This turns

the somites into blocks, deeper than they are wide (Figure 1B). While the mesoderm is moving toward the midline, the endoderm and the neural ectoderm follow it; thus, the flat embryonic shield is transformed into a rounded embryo.

When the somites are flat and only two or three cells thick, they show no organization. Later on, as they deepen they develop a single-celled cortex around an unorganized interior. The cortex first forms next to the notochord and then encircles the entire somite. Its cells are slightly columnar on the notochord side, shortening to cuboidal on the exterior side.

The somite masses begin to subdivide in the anterior part of the body at 68 hours. This is the first step in the formation of the individual muscle fibers. The somites split into strips that run parallel to the long axis of the embryo and extend from the notochord to the outer walls of the somites (Figure 1B). This divides the somites into five or six layers and obliterates the cortex.

Subdivision continues; the planes now run at right angles to the previous ones, slicing the somites from top to bottom. At 88 hours, the somites consist of ribbons one cell thick and four or five cells long. The single-cell muscle fibers do not develop until after hatching. By 70 hours, each somite already has developed a V-arch with the apex directed forward and is inclined toward the notochord. By 77 hours, a small constriction in the center of the somites begins to divide them into dorsal and ventral halves corresponding to the epaxial and hypaxial trunk musculature of the adult (Figure 1C). The small cells present at the neck of the constriction between the two halves become connective tissue, presumably that of the skeletogenous septum of the adult fish (Wilson, 1891).

The somite fibers are able to contract as early as 83 hours, when the embryos twitch occasionally. Contractions become more frequent and violent, so that by 92 hours the embryo may twist around inside the egg membrane.

Heart and Circulatory System

The degree of development of the heart and blood vessels at hatching varies in different fishes. Larvae newly hatched from demersal eggs have a complete and complicated circulatory system. Those from pelagic eggs have poorly developed circulatory systems.

The English sole, a member of the latter class, has a well-developed and differentiated heart at hatching, but the aorta is the only blood vessel present. There are no veins to return blood to the heart; hence, the circulation is incomplete.

Heart Formation

The mode of heart development also varies among fishes. Ryder (1887) supplies some information on the comparative development of this organ.

In the English sole at 62 hours, a slight bulge on the ventral body margin just behind the eyes marks the heart anlage. It is a concentration of mesoderm cells ventral to the notochord and anterior to the

foregut. A lumen appears in it around 67 hours, transforming it into a short, straight tube, the anterior end of which becomes the venous part of the heart and the posterior end the arterial. At this time, the postcardiac membrane running from behind the heart up to the auditory sacs separates the heart from the posterior body (Figure 3D). At 70 hours, the anterior end has widened, giving the heart a funnel shape. Subsequently, the anterior venous end bends and grows toward the left. In several fishes, for example *Gadus morrhua* and *Alosa sapidissima* (Ryder, 1884), the venous end turns and grows backwards, but in the English sole it remains on the embryo's left side.

By 70 hours, the heart begins to differentiate into its various parts: sinus venosus, auricle, ventricle, and conus arteriosus; and by 74 hours, weak and widely separated pulsations may occur. Steady but feeble beating is established by 77 hours, and by 83 hours the heart is contracting strongly.

Ventrally, the heart touches the periblast and is surrounded by the pericardial space, which is continuous with the remains of the subgerminal cavity (Ryder, 1884). Blood cells bud off from the periblast (Ryder, 1882*b*, 1884, and 1887) and enter the venous end of the heart, which opens out into the pericardium. Blood islands in the yolk and a blood string near the notochord give rise to the blood cells in *Fundulus heteroclitus* (Stockard, 1915); however, nothing definite can be said about the method of formation in the English sole, since no developing blood cells were seen.

As the yolk is absorbed, it is carried into the heart and dispersed through the embryo (Ryder, 1884; 1887). There is a close connection between the yolk sac and heart in English sole larvae, and as the sac grows smaller, a lobe of it sometimes projects toward the heart.

Aorta

The aorta first opens at approximately 79 hours. Mesenchyme cells migrate posteriorly from the heart under the subnotochordal rod and separate to enclose a central space (Figure 1C). In general, the nuclei of the aortal cells lie on the dorsal and ventral sides of the aorta and thin cellular extensions connect them laterally. The aorta is first open intermittently and at hatching this is still the condition in the tail.

No other blood vessels arise until after hatching.

Coelomic Mesoderm and Pronephros

At 55 hours, a furrow appears in the dorsal margin of the mesoderm. It deepens and divides the mesoderm into somitic and coelomic portions. The somitic part lies adjacent to the notochord and the neural cord, while the thin coelomic layer lies next to the periblast. No cavity develops in the coelomic mesoderm during embryonic life, but that portion next to the gut separates into dorsal and ventral sections. The dorsal section, the pronephros or embryonic kidney, constricts off from the ventral section as a rounded mass of cells (Figure 1C). At hatching, the pronephros stretches from the pectoral fin buds to the hindgut. Its cells have assumed a radial arrangement but have not yet separated to open the Wolffian duct, the functional equivalent of the ureters of higher vertebrates.

The ventral section of the coelomic mesoderm, a flattened plate two cells thick, forms the coelom after hatching, presumably by the separation of the two-cell layers.

Gonads

The gonads do not form during the embryonic life of the English sole. Little work has been done on their formation in teleosts. In general, it may be said that their site of origin is between the dorsal mesentery and the anterior part of the mesonephric kidney (Nelsen, 1953).

Pectoral Fins

The pectoral fin mesoderm grows out from the tip of the coelomic mesoderm, situated somewhat posterior to the auditory sacs. The fins appear at 85 hours and become dorso-lateral projections, two to three cells thick. Dorsally, they are covered with ectoderm, ventrally they border the periblast. At hatching, when the fin fold ectoderm separates from the body it also detaches from the dorsal side of the pectoral fins, leaving them in contact with the subdermal space. In the newly hatched larva, they rest on the yolk sac and extend backward along the sides of the larva (Figure 3F). They appear to be free from the larval body but are actually still enclosed by the trunk ectoderm.

ORGANS OF ECTODERMAL ORIGIN

Brain and Spinal Cord

Neural Ectoderm and Keel

The neural ectoderm forming the dorsal section of the embryonic shield is thicker than the extra-embryonic ectoderm. It increases in thickness as the ectoderm cells move toward the midline of the embryonic shield, creating a deep keel that is especially well developed at the shield's anterior end—the future brain. The early brain appears in living eggs as a pronounced ventral swelling (Figure 2C).

In sections, the cells of the early neural keel appear fusiform and run ventro-laterally from an apex in the dorsal midline. In the brain region, the deeper cells of the keel run more or less straight across it. A temporary dorsal furrow exists in the anterior neural keel prior to blastopore closure.

Two basic changes occur in the nervous tissues: (i) the main areas of the brain are defined by constrictions; (ii) the cells simultaneously rearrange themselves to permit the opening of the brain ventricles and the neural or spinal canal.

Brain Subdivision

At blastopore closure, none of the primary brain regions has differentiated. The brain swells out markedly just posterior to the eyes, but this does not distinguish the midbrain from the hindbrain. At 66 hours, a slight indentation appears just behind the eyes. It deepens and by 70 hours becomes a constriction separating these areas. The hindbrain or medulla also develops a cerebellar fold posterior to this constriction that further identifies it. Another constriction beginning at 66 hours and complete at 79 hours divides the forebrain from the midbrain.

Ventricle and Canal Formation

Complicated internal changes occur in the cellular arrangement of the nervous tissues. The original ventrolateral or V-arch cell pattern of the neural keel gives way to a U-arch arrangement, and finally the cells run straight across the keel. They next separate into two columns at 55 hours, one on each side of the brain and neural keel (Figure 1B). But, as yet, no space exists between them. These changes begin in the forebrain and continue posteriorly.

The formation of the neural canal begins in the medulla at 74 hours. The cells at the ventral end of the brain pull apart to open a small, round space. The opening moves down the neural chord and reaches near the tail tip by the time of hatching. This cavity remains small and is restricted to the ventral part of the cord. The only other brain cavities that open before hatching are the third ventricle, arising at 74 hours between the forebrain and midbrain, and the dorsal part of the fourth ventricle in the medulla, which opens at 79 hours. These ventricles are broad, shallow spaces roofed with neural ectoderm.

Besides changing position, the brain cells become much smaller, more numerous, and densely packed. The brain walls increase from two to four to six to eight cells in thickness. Similar changes take place in the neural cord and spread posteriorly, although the cord walls in the posterior tail are still only one or two cells thick at hatching.

Infundibulum

The infundibulum arises as an outgrowth from the ventral part of the posterior diencephalon (the posterior part of the forebrain) at approximately 79 hours. It separates from the forebrain and rounds up. Its cells assume a radial arrangement and grow posteriorly. The fusion of the infundibulum with Rathke's pouch (a postembryonic evagination from the roof of the mouth) to form the pituitary gland takes place after hatching.

Eyes

At 42 hours, the eye vesicles arise as lateral swellings from the forebrain. Initially, they are continuous with the brain but soon begin to split away from it and from the head ectoderm. By the time of blastopore closure, the separation is complete except for the optic stalk connecting them to the forebrain. A thin mesenchymal layer intervenes between the vesicles and the brain, and a central longitudinal fissure, from which the cells radiate outward, splits the vesicles. This fissure does not widen into a space; hence, the term "vesicle" is actually inappropriate.

At 66 hours, the dorso-lateral ectoderm over the eyes thickens and pushes inward to form the lens. It flattens and indents the vesicles, transforming them into the optic cups. The eye vesicle cells between the eye fissure and the brain are greatly flattened when this happens. These flattened cells become the retina (Figure 1E).

Originally, the lens is a plate of columnar cells but as it pushes deeper into the optic cups it rounds up. Later, it differentiates into an external single-celled cortex and an inner group of circularly wound cells (Figure 1E).

In cross section, the optic cups surround the lens on three sides and partly overlap it on the fourth by 90 hours. Splitting the ventral side of the optic cups below the lens is the choroid fissure, through which blood vessels later enter the eye. The cortex of the lens disappears on the inner side and is restricted to the part of the lens not covered by the optic cups at hatching. The inner lens cells elongate and wind around each other very tightly. They form the spherical refracting body of the lens.

Olfactory Sacs

As early as 47 hours, cell masses appear on either side of the forebrain and in front of the eye vesicles. They separate from the ectoderm around them, assume a rounded triangular shape, and develop a shallow pit on the ventro-lateral border (Figure 3B). The cells are originally fusiform and radiate from the pit; however, they later become somewhat rounded and more numerous and the radiating arrangement is partly lost. This sensory pit, which also penetrates the surface ectoderm of the embryo, increases in diameter but otherwise does not change. The sacs are connected to the forebrain by the olfactory nerves and are separated from the eyes by a thin strip of head mesenchyme. This is the condition at hatching.

Branchial and Lateral Line Sense Organs and Auditory Vesicles

The lateral ectoderm posterior to the eyes and anterior to the somites thickens and invaginates slightly, forming the sensory furrow shortly before the closure of the blastopore. At three points along the furrows, the invagination produces a mass of cells which transforms into sense organs. The anteriormost point is immediately behind the eyes, where the branchial sense organ develops (Figure 3B); the second point is the auditory vesicle (Figures 1D, 3D, and 3F); and the third is the lateral line organ (Figure 1C). By time of hatching, the lateral line organ has migrated posteriorly and stretches from the middle of the yolk sac almost to the hindgut.

The first of these structures to become visible in living eggs is the branchial sense organ at 55 hours. While the lateral line organ can be seen at this time in whole mounts, it cannot be observed in living eggs because of its position and transparency. The auditory vesicle appears at 60 hours.

Both the branchial and lateral line organs arise as clusters of fusiform cells radiating from a point on the surface ectoderm. Their nuclei become basal in location, small pits appear at their junction with the ectoderm, and short sensory hairs project from these pits a few hours before hatching.

Auditory Vesicles

In living eggs, the first indications of the auditory vesicles are seen at 60 hours. They become conspicuous 8 hours later as grayish, elliptical vesicles dorsal and lateral to the medulla just above the gill slit (Figure 3D).

Sections reveal them as early as 55 hours as thickenings of the ectodermal wings lateral to the main body mass. These ectoderm plates grow medially and ventrally toward the hindbrain. When they reach it,

they close over dorsally and form heart-shaped sacs. The walls of the sacs are orginally composed of a single layer of columnar cells enclosing a small central cavity which runs parallel to the longitudinal axis of the embryo. Subsequently, the cells in contact with the brain flatten; the central cavity enlarges, becomes elliptical in transverse sections, and inclines at an angle to the horizontal. The vesicles as a whole become elliptical in cross section. Meanwhile, the medulla grows over the vesicles. Then, the roofs of the vesicles are reduced to a membrane and the floors thicken until they are two cuboidal cells deep. This is the condition of the vesicles at hatching (Figure 1D).

Otoliths arise at 83 hours as small dark circles at the anterior and posterior ends of the vesicles (Figure 3D). They are composed of calcium carbonate which the preservative dissolves; hence, they are not seen in sections. By hatching, they have enlarged but otherwise remain unchanged.

Gills

Only one gill slit is formed in the embryo (Figure 3D). It appears at approximately 65 hours as a shallow ectodermal inpushing below the auditory sacs. Subsequently, it deepens and cuts toward the midline. Shortly before hatching, it meets an endodermal outgrowth from the foregut and fuses with it (Figure 1D). This establishes an almost horizontal slit or canal under the auditory sacs and notochord.

No additional gill slits were seen to develop in the larvae up to 14 days after hatching. Budd (1940) neither mentions nor illustrates additional gill slits. As most teleosts form five gill slits during larval life, their apparent absence in the English sole may simply be due to extreme difficulty in observing them.

Ectoderm and Fin Fold

At blastopore closure, two layers of flattened ectoderm cells cover the yolk. The outer one is derived from the epithelium of the blastoderm and the inner one from the blastoderm cells that did not invaginate. Over the embryo, the inner layer is continuous with the neural ectoderm.

Gradually, the ectoderm separates from the embryo, first over the mesoderm and then over the neural keel (Figure 1B). A space arises between the mesoderm and the ectoderm, but the mutually distinguishable ectoderm and neural keel remain in contact. At the same time, the outer epithelial layer disappears.

The ectoderm thickens in the tail (the cells become cuboidal and a second layer forms) and invaginates down the sides, beginning at the tip and progressing anteriorly. The invaginating folds from opposite sides meet and fuse in the ventral midline at 68 hours, ensheathing the tail in ectoderm and freeing it from the yolk. Beneath the embryo, the yolk is also covered with ectoderm arising from the fusion of the lower halves of the ectodermal inpushings. Anterior to the tail, the ectoderm over the head and body also invaginates but does not push under the embryo; hence, these areas remain in contact with the yolk.

Shortly before the fusion of the ectodermal tail invaginations, the thick ectoderm at the tail tip (which looks like a projecting nub) splits to form a groove. The groove moves up the tail midline, first on the

dorsal and later on the ventral side. The ectoderm immediately adjacent to these grooves is noticeably thicker than the more lateral ectoderm.

To create the fin fold, the ectoderm around the grooves pulls away from the embryo, forming folds on the dorsal and ventral sides of the embryo (Figure 1C). These folds are composed of two layers of spindle-shaped cells, the outer layer of which develops vacuoles before hatching. The cavities between the folds and the embryo are the subdermal spaces. They are soon invaded by threads of connective tissue and, after hatching, by mesenchyme cells that build the fin rays.

Laterally, the ectoderm adheres or almost adheres to the sides of the embryonic tail. On top of the body, where only a dorsal fin fold exists, the ectoderm is in contact with only the dorso-lateral margin of the myotomes and spinal cord (Figure 1C).

Chromatophores

Chromatophores originate from the neural crest cells, which connect the neural keel to the ectoderm above it. Cells from the neural crest loosen and migrate to other areas of the embryo, differentiating into chromatophores both during and after migration (Shepard, 1961).

In the English sole, fully developed chromatophores occur all along the neural crest, occasionally between the mesoderm and neural keel, more commonly between the ectoderm and the mesoderm, but never around the notochord (Figures 1B and 1C). From this, I suspect that the main pathway followed by these cells passes between the ectoderm and mesoderm rather than between the mesoderm and the neural keel, as in some other species. The presence of melanoblasts would solve the question, but I could not find any.

In *Fundulus heteroclitus* the yolk sac becomes permanently pigmented by chromatophores from the extraembryonic germ ring (Stockard, 1915). The occasional and temporary yolk chromatophores of the English sole may or may not have a similar origin.

Pigmentation

Small, round melanophores are scattered over the posterior dorsal surface of the head and the anterior dorsal surface of the body a few hours after blastopore closure. They remain small and inconspicuous until 57 hours, when they enlarge. At this stage, they have various shapes—rectangular, square, or elliptical, but never stellate or dendritic. The melanophores tend to be situated at the lateral edges of the neural ectoderm and this gives them a rough linear arrangement. They never clump together but remain well spaced.

As time goes on, the chromatophores become larger and more numerous. They spread down the body and tail, reaching the tip of the tail at 70 hours; soon afterward, they invade the anterior half of the head. The first stellate melanophores now appear and the first amber chromatophores or xanthophores develop. The latter are very diffuse and may form a very pale yellow band on the sides of the embryo. Over the eyes and brain, the xanthophores are dendritic.

At 76 hours, the melanophores have grown still larger and occasionally show dendritic extensions. A few of them migrate to the yolk, from which they disappear before hatching. The amber pigment spots

have spread to the tail tip and are now most prominent on the posterior third of the tail, where they fuse into a yellow band. The black chromatophores are always more numerous than the yellow.

A diffuse yellow band halfway down the side of the tail characterizes the newly hatched larvae. This band sometimes appears as a row of almost united xanthophores. Melanophores are evenly distributed on the dorsal and ventral margins of the tail. They are rarely present in a lateral position. The head shows a variable scattering of black and yellow pigment spots. There are few chromatophores on the extreme tail tip, few on the lateral sides of the tail, and none on the yolk sac or fin folds (Figure 2D).

ORGANS OF ENDODERMAL ORIGIN

Alimentary Canal

The endoderm invaginates as a single layer of cells under the mesoderm and, insofar as I can determine, under the notochord as well. In some fishes, like the black sea bass, *Centropristes striatus*, the endoderm is not originally present under the notochord but converges towards it later on (Wilson, 1891). In other fishes, e.g., the Spanish mackerel, *Scomberomorus maculatus*, it is always under the notochord (Ryder, 1882*a*).

The endoderm remains as a thin plate under the other tissues until after blastopore closure. Then, as the embryo rounds up, it crowds toward the midline and forms a column under the notochord with lateral and evershortening wings under the mesoderm. By 56 hours, the lateral endodermal wings are short and a solid gut cord has formed. The cells pull away from each other in another hour and a central lumen appears (Figure 1B). The wings are absorbed and the gut rounds up to form a tube of a columnar cells (Figure 1C).

The alimentary canal of the cod also forms in this manner (Ryder, 1884). But the gut lumen of the sea bass results from the fusion of lateral folds of endoderm (Wilson, 1891).

In living English sole embryos, the alimentary canal first appears as a series of zigzagging pouches separated by constrictions. The constrictions disappear in a few hours, leaving the gut straight and smooth (Figure 3C).

The gut lumen opens first in the anterior somitic region and then moves quickly down the tail, reaching the last somite at 60 hours. Subsequently, it follows the posterior march of the somites. At 77 hours, the hindgut dips ventrally and the anus breaks through the fin-fold ectoderm below the last somite. The embryonic tail is twisted around so that its dorso-ventral axis lies parallel to the yolk surface, instead of at a right angle to it. Hence, when the anus breaks through the fin fold, the hindgut is free to grow over the yolk, carrying the fin fold with it. A loose string of ectoderm cells precedes the growth of the hindgut. These cells unite the fin fold around the hindgut to the posterior and ventral side of the yolk sac (Figure 3E).

Posterior to the hindgut, endoderm still exists. It tubulates to form the postanal gut and then degenerates. At hatching, the area between the ventral borders of the somites and below the aorta contains a few endoderm cells which still surround a lumen in places.

Subnotochordal Rod

When the endoderm cells concentrate toward the midline, the most dorsal gut cells pinch off as an evagination (Figure 1B). This creates the subnotochordal rod, a single-cell string of flattened cells sandwiched between the gut and the notochord. Posteriorly, this rod merges with the endoderm of the floor of Kupffer's vesicle. Anteriorly, it extends as far as the gut does. The rod disappears as the aorta develops. At hatching, it still persists in the posterior part of the tail.

Kupffer's Vesicle

Kupffer's vesicle is a common and conspicuous feature in the embryonic tails of teleosts. As previously mentioned, it appears at 46 hours as a small, clear, round vesicle not far from the germ ring. It reaches its maximum size 1 or 2 hours after blastopore closure, when it protrudes into the yolk as a clear vesicle near the tail tip, posterior to the notochord and somites (Figure 3A). It extends deep into the embryo, where its floor is composed of columnar cells continuous with those of the still solid gut. The fluid contents of the vesicle are believed to be partly digested yolk broken down by the periblastic nuclei. The periblast itself roofs over the vesicle and occasionally forms a thickened cap on it. From its contents and from its position posterior to the last somite, it has been concluded that Kupffer's vesicle furnishes material for the growth of the embryo (Sumner, 1900).

As the somites move down the tail and pass Kupffer's vesicle, it diminishes in size. There is considerable variation in the time of its disappearance, which may occur anywhere from 60 to 73 hours. However, some newly hatched larvae have a large vesicle attached to the hindgut and extending into the yolk sac. In these, the vesicle (provided it is Kupffer's vesicle) persists for perhaps 12 hours more.

As Kupffer's vesicle grows smaller, internal changes take place in its walls. The vesicle's original shape within the embryo is a deep U or V in cross section. It is lined with endoderm cells which extend laterally under the mesoderm. Dorsally, the endoderm flows into the material of the undifferentiated notochord and neural keel. This area of fused neural ectoderm and endoderm is called the neurenteric streak. When the notochord and somites form in this region, they push the endodermal lining ventrally and medially until the cavity of Kupffer's vesicle is obliterated. The gut lumen then opens and runs through the previously solid endodermal mass.

Rare abnormalities occur in which Kupffer's vesical reaches tremendous proportions. In these embryos, the tail is abnormally short and is covered in large part by the vesicle, which is ringed by smaller vesicles. The gut is abnormally thick and ends in the vesicle.

Caudal Vesicle

The caudal vesicle is a virtually unknown structure. Although it is not of endodermal origin it is discussed here because of its relation to Kupffer's vesicle. It probably has not been described before as it occurs in the English sole, although accounts of similar vesicles in other fishes exist.

At 46 hours the closing blastopore is not plugged by yolk, but by a thick bulge of periblast. Capping the periblastic plug are large nuclei and a platelike vesicle filled with material that stains pink in eosin, rather like the yolk. As the blastopore closes, the vesicle rounds up and protrudes into the dwindling aperture. When the blastopore lips fuse, the vesicle moves to the ventral tip of the embryonic tail a short distance posterior to Kupffer's vesicle, to which it is connected by a thickened ridge of periblast (Figure 3A). Originally, the periblast lies between the caudal vesicle and the yolk; however, in the course of migration places are switched and the periblast now separates the vesicle from the embryo. The caudal vesicle becomes visible in living embryos after blastopore closure as a coagulated bump or spot under the tail tip.

The vesicle continues to move toward Kupffer's vesicle, but it never quite fuses with it. However, the caudal vesicle sometimes develops a clear globule on its anterior end that gives the impression that fusion has occurred. It dwindles in size and becomes filled with irregular droplets or vesicles that fail to stain in eosin. This gives the vesicle a reticulated appearance in sections and a coagulated one in living embryos (Figure 3A). The boundary which formerly restricted it from the periblast becomes indistinct and the ectoderm of the fin fold grows between it and the embryo. Generally, it is last seen between 67 and 78 hours, ventral or slightly posterior to the remains of Kupffer's vesicle.

LARVAE

Hatching

The first eggs hatch at approximately 98 hours and the last at about 108 hours. Most eggs sink to the bottom of the containers shortly before hatching, a few hatch in midwater. Periods of violent flexing of the tail and spinning around of the whole embryo within the egg membrane alternate with longer periods of rest. Hatching is generally head first; nevertheless, a few embryos were seen with their tails protruding instead of their heads. The embryo often stops moving after the membrane has been broken and lies half in and half out of the shell.

Many teleosteans develop hatching glands, the enzymes of which dissolve the egg membrane (Brown, 1957). In some species, the enzyme secreting sites are distributed over the head and the anterior third of the yolk sac, while in others the hatching glands are unicellular and line the pharynx; however, I observed neither type of structure in the English sole.

Newly Hatched Larvae

Immediately after hatching, the larvae drift to the surface, where they float on their sides or yolk sac up. Occasionally, their bodies are bent at the hindgut, a retention of the embryonic position.

Living, newly hatched larvae average 2.85 mm in total length, and the oval yolk sac extends slightly less than half this length (Figure 2D). The head is still attached to the yolk sac and bends ventrally as it follows the yolk sac's curve. The eyes are unpigmented, the mouth and anus have not opened, and the larvae lack jaws. Membranous rudiments of the pectoral fins extend backward over the yolk sac. They reach from the level of the auditory vesicles to the middle of the yolk sac. The

dorsal fin fold begins at the back of the head, is narrower on top of the body than on top of the tail, and is about the same width as the midtail. The ventral fin fold is widest at the hindgut, narrowing progressively toward the tail tip.

Three-day Larvae

After 3 days, the larvae have grown to 4.32 mm. There are two separate bands of yellow pigment around the middle of the tail and another band around the hindgut. A small yellow splotch colors the body at the pectoral fin level. Melanophores are distributed over the dorsal and ventral margins of the body and the tail, with a few over the brain and auditory sacs. They are rounded and have short radiating extensions.

The head is free of the yolk sac and the eyes are slightly grayish and ringed with xanthophores. The pectoral fins are free of the body. The enlarged auditory sacs are just posterior to the eyes, closer than they were at hatching. The liver and gall bladder have formed, the latter as a clear vesicle lateral to the liver, which in turn is below the gut and anterior to the yolk sac. Between the midbrain and the forebrain lies the pineal body. The brain itself is more rounded. The mouth and anus are still closed, but the foregut has grown into the head.

The larvae can swim for 2 or 3 inches, but usually they hang head downward in midwater. A few rest on the bottom.

Six-day Larvae

The larvae have grown to 4.53 mm. There are still two dense yellow bands on the tail, one on the posterior third and one, less dense, anterior to the middle of the tail. The tail and body melanophores, which are frequently fused, are elongated antero-posteriorly and have lateral dendritic processes. Melanophores are now over the ventral margin of the yolk sac and on the ventral body wall below the heart. A few xanthophores are over the liver and gill slit area and around the eyes. A single melanophore is usually located on the posterior angle of the mandible. The optic cups are black and the lenses are yellow-gray.

The mouth is open, and the mandible and maxillary are fairly well developed. The fan-shaped pectoral fins flutter. Posterior to the gut, the urinary vesicle bends downward from the pronephric mesoderm and opens at the margin of the ventral fin fold. The anus is still closed. Because the yolk sac is shrinking, a space has appeared between it and the hindgut, and the fin fold ectoderm has begun to grow underneath it. The yolk sac is now small, elliptical, and well separated from the head. Fin rays are developing in the lobe of the fin fold at the tail tip. The auditory vesicles are concave on the ventral side.

The larvae are still weak swimmers.

Nine-day Larvae

There has been a slight increase in length to 4.58 mm.[2] On the tail, melanophores are more numerous on the ventral than on the dorsal margin. The entire tail except the tip may be solid yellow. There are

[2] Since the larvae were not fed, descriptions of the 9- to 14-day stages might not fit larvae caught in plankton hauls.

fewer xanthophores over the hindgut. Anterior to the hindgut, dendritic melanophores are strung out under the notochord up to the level of the auditory sacs. The melanophores ventral to the heart have enlarged and spread posteriorly. Xanthophores no longer ring the eyes. Both the optic cups and the lenses are black.

The heart is located between the lower jaw and the liver. Canals have appeared in the auditory vesicles. Just posterior to the latter structures, the clavicle is present as a hoop-shaped ring that causes this part of the body to expand. The gut has become convoluted and has a very wide lumen. Peristalsis occurs. The anus is probably open. The yolk sac is very small or absent, and the fin fold and the expanded gut occupy its former position.

Most larvae rest with their heads touching the bottom or lie on their sides. They seldom swim.

Twelve-day Larvae

Tail pigmentation has not changed, but head and body pigmentation is usually reduced. Few other changes have occurred; the gall bladder has enlarged and the fin rays have grown a short distance anteriorly along the tail. Ten larvae averaged 4.60 mm in length. This increase is probably due to chance variability in measurements rather than actual growth.

Fourteen-day Larvae

Pigmentation is variable: it may be the same as at 12 days or it may be reduced. When reduced, melanophores may be almost entirely absent from the tail. There is little or no pigment on the hindgut and little on the body—a few melanophores on the ventral side. One or two xanthophores remain on the head. The only notable changes are a concavity in the region of the former yolk sac and a decrease in size to 4.18 mm (Figure 2E). Both are probably caused by utilization of body tissues as a food source. The last unfed larvae die at this stage.

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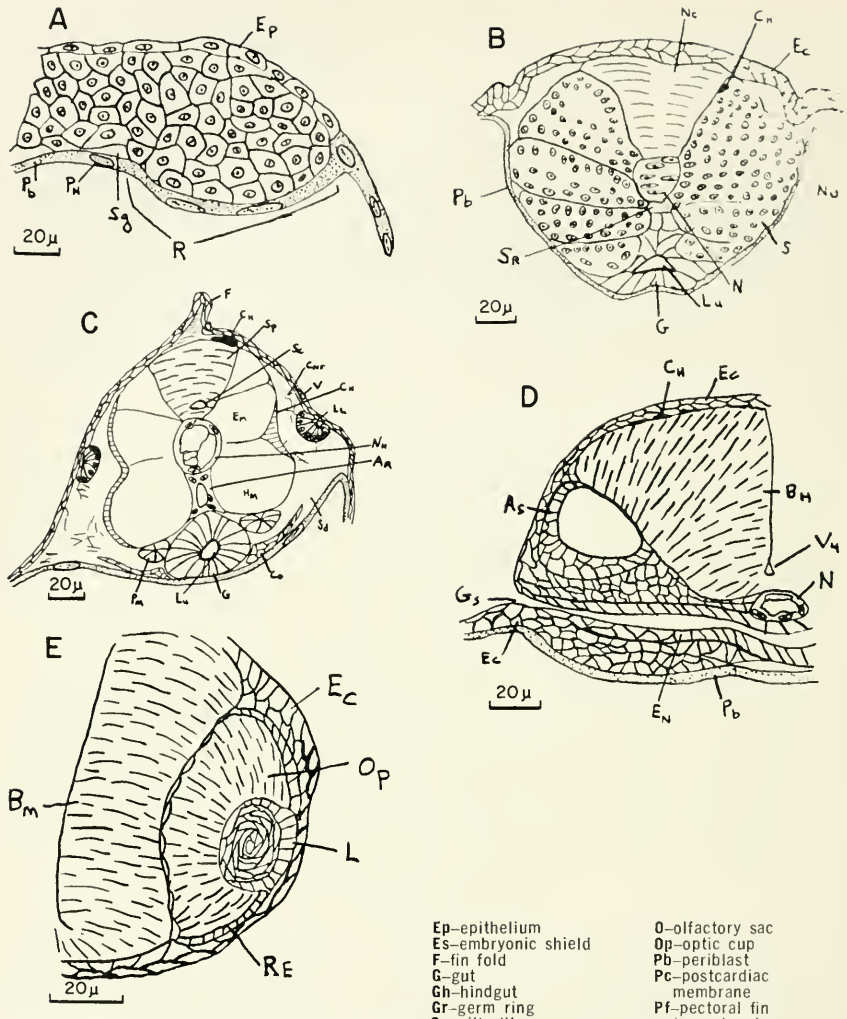

The drawings are semidiagrammatic. In many organs, the pattern of cell arrangement is indicated by lines or by the presence of nuclei. Blank tissues mean that there is no relevant or easily reproducible arrangement of cells.

ABBREVIATIONS USED IN THE ILLUSTRATIONS

A–anus
Ar–aorta
AS–auditory sac
Bh–hindbrain
Bm–midbrain
Br–brain
Bs–branchial sense organ
Ch–chromatophore
Cn–connective tissue
Cnf–connective tissue fibers
Co–coelomic mesoderm
Cv–caudal vesicle
Ec–ectoderm
Em–epaxial region of somite
En–endoderm
Ep–epithelium
Es–embryonic shield
F–fin fold
G–gut
Gh–hindgut
Gr–germ ring
Gs–gill slit
H–heart
Hm–hypaxial region of somite
Kv–Kupffer's vesicle
L–lens
Ld–dorsal lip of the blastopore
Ll–lateral line organ
Lu–lumen
Lv–ventral lip of the blastopore
M–melanophore
N–notochord
Nc–neural cord
Nh–notochordal sheath
Nu–nucleus
O–olfactory sac
Op–optic cup
Pb–periblast
Pc–postcardiac membrane
Pf–pectoral fin (mesoderm)
Pm–pronephric mesoderm
Pn–periblast nuclei
Pv–perivitelline space
R–rand wulst
Re–retinal layer
S–somite
Sc–spinal canal
Sd–subdermal space
Sg–subgerminal cavity
Sp–spinal cord
Sr–subnotochordal rod
V–vacuole
V4–fourth ventricle
Y–yolk
Ys–yolk sac

FIGURE 1—A, 23 hours, edge of blastodermal cap shawing *rand wulst* (transverse); B, 68.5 hours, midbady of embrya (transverse); C, 102.5 hours, midbody of embryo at hatching (transverse); D, 102.5 haurs, hindbrain, auditary sacs, and gill slit at hatching (transverse); E, 102.5 hours, optic cup and differentiating lens at hatching (frontal).

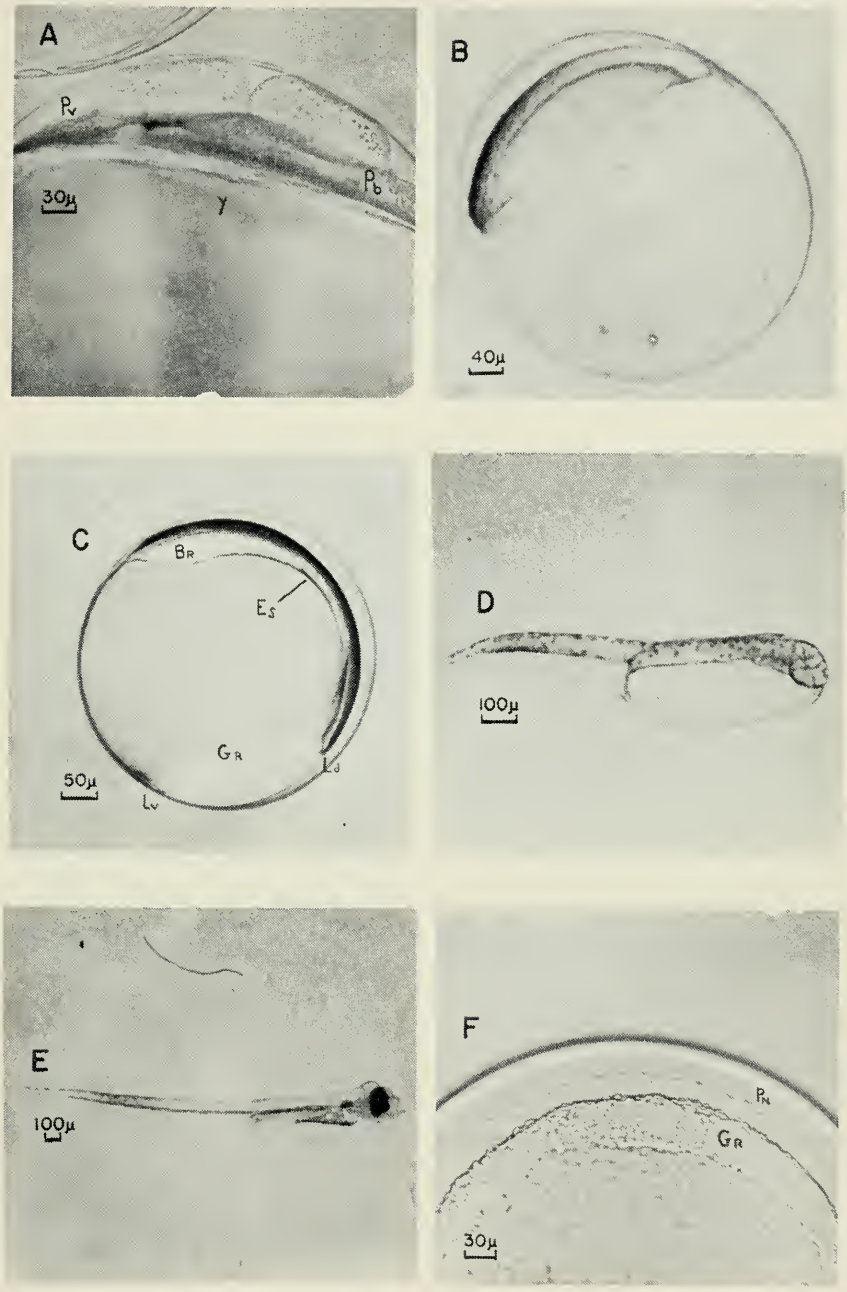

FIGURE 2—A, 3 hours, two-cell stage (lateral); B, 23 hours, hollow blastodermal cap (lateral); C, 42.5 hours, embryonic shield; D, newly hatched larva; E, 14-day larva; F, 24 hours, edge of germ ring and periblast nuclei (dorsal).

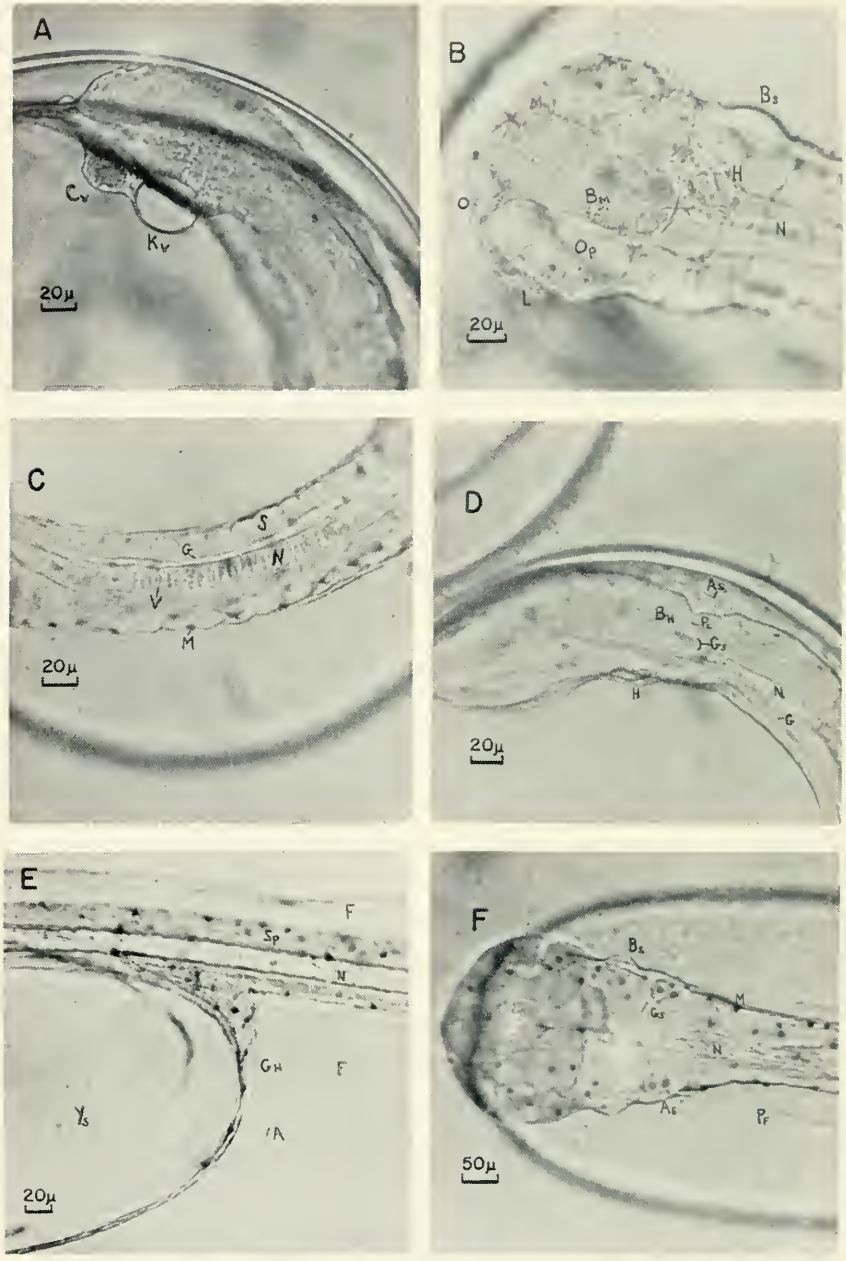

FIGURE 3—A, 64 hours, Kupffer's and caudal vesicles (lateral and posterior); B, 88 hours, head (dorsal); C, 84 hours, midbody with late gut (ventral), head on the right; D, 74.5 hours, anterior body (lateral); E, 109 hours, posterior yolk sac and hindgut of newly hatched larvae; F, 100 hours, head and anterior body of newly hatched larva (ventral).

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ORGANOGENESIS IN THE WALLEYE SURFPERCH, *HYPERPROSOPON ARGENTEUM* (GIBBONS)[1]

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Major variations in the development of this species occur in the digestive and cardiovascular systems. These unusual features are probably characteristic of all members of the family Embiotocidae.

Modifications in the digestive system include the early opening of the first gill cleft, the development of tall columnar epithelium with associated flagellar-like structures in the esophageal region, and a tremendous enlargement of the hindgut containing many long villi.

The heart develops from a solid cell mass just anterior to the yolk. Early in development, the sinus venosus envelops the yolk except dorsally where it lies adjacent to the liver. This places the yolk in direct contact with the blood circulating through the heart. With the formation of the septum separating the pericardial and peritoneal cavities, the yolk becomes associated with the liver and lies next to the hepatic vein. It continues to remain closely allied with the hepatic vein until the yolk substance is completely absorbed.

INTRODUCTION

The viviparous Embiotocidae began to attract interest around the year 1852. In the following years a number of papers describing new species were published, but no definitive work was done on their embryology until the studies of J. A. Ryder and especially Carl H. Eigenmann in the 1880's and 1890's. Subsequently, little has been published on the embryological aspects of these very interesting fishes.

One fascinating characteristic of these fishes is their ability to provide nutrients to the young in addition to those supplied in the yolk. Food material is apparently derived from the lining cells of the ovary itself, and includes actual cells that can be seen in the gut lumen. The first gill cleft opens before hatching and it is through this opening that the secretory products first enter the alimentary tract. Later this function is assumed by the mouth, but during this early period no oral opening is present.

Since specimens used in this study were caught with hook and line, the stages represented do not form as complete a series as might be desired. Nevertheless, enough specimens were studied to give a reasonably clear picture of the organogenesis of this species.

The fish were caught in the vicinity of Newport Beach, Orange County, California, mostly from Balboa Pier. I am particularly indebted to my son Don, who accompanied me on the many necessary fishing trips, as well as to others who kindly donated specimens.

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METHODS

Whole mounts and serial sections were used in this study. The major effort was confined to the study of serial sections made at different stages of development.

All material was fixed in 10% formalin in tap water. The whole mounts were stained with borax-carmine, and the serial sections cut at 10 microns and stained with hematoxylin and triosin.

The borax-carmine stains proved to be of great value in the preparation of the serial sections. This staining was done during dehydration before embedding. The eggs and early embryos are very small, but staining made their internal anatomy visible and it was relatively easy to orient them for proper sectioning. Following sectioning, the borax-carmine again demonstrated its worth because the cut specimens could be seen in the paraffin ribbon and cutting was much simplified. The borax-carmine washed out during the subsequent staining procedure and did not affect the final results.

Measurements were made on formalin preserved material, using two types of measurement. Somite counts were made before hatching, since the embryo lies in a curved position around the yolk. Hatching was not observed, but probably occurs between $1\frac{1}{2}$ and 2 mm. Standard length was used in all subsequent determinations.

EARLY DEVELOPMENT

The eggs are released into the ovarian cavity in November or early December, and the young are born in May or early June. This results in a gestation period of between five and six months. The eggs and young are not attached to the mother but lie free among the ovarian folds. The developing young are positioned in a random manner, some in a head-forward direction and others with the head lying posteriorly.

The diameter of the egg membrane measures about 0.7 mm and the germinal portion about 0.5 mm, with the perivitelline space intervening.

The earliest developmental stage procured was an early blastula in which the cells of the periblast had separated from the blastoderm and a beginning blastocoele was forming between these two structures (Figure 1A). Even at this early stage the cells had largely overgrown the yolk.

During gastrulation the hypoblast is formed and moves forward from the dorsal region of the blastopore (Figure 1B). The neural keel differentiates very early and in cross sections is easily identified even in the region close to the blastopore (Figure 1C). The blastocoele remains as a prominent feature in this stage, and the primitive gonadal cells are first observed as large cells with definite acidophilic cytoplasm (Figure 1D). Following closure of the blastopore, the embryo elongates and further differentiation with somite formation occurs.

ORGANOGENESIS

The Integument and Appendages

The epidermis is very thin before the formation of the scales and consists of only a few layers of cells. Scales are relatively late in development. A thin plate of bony material is formed just beneath the surface epithelium, which becomes elevated at the posterior margin of

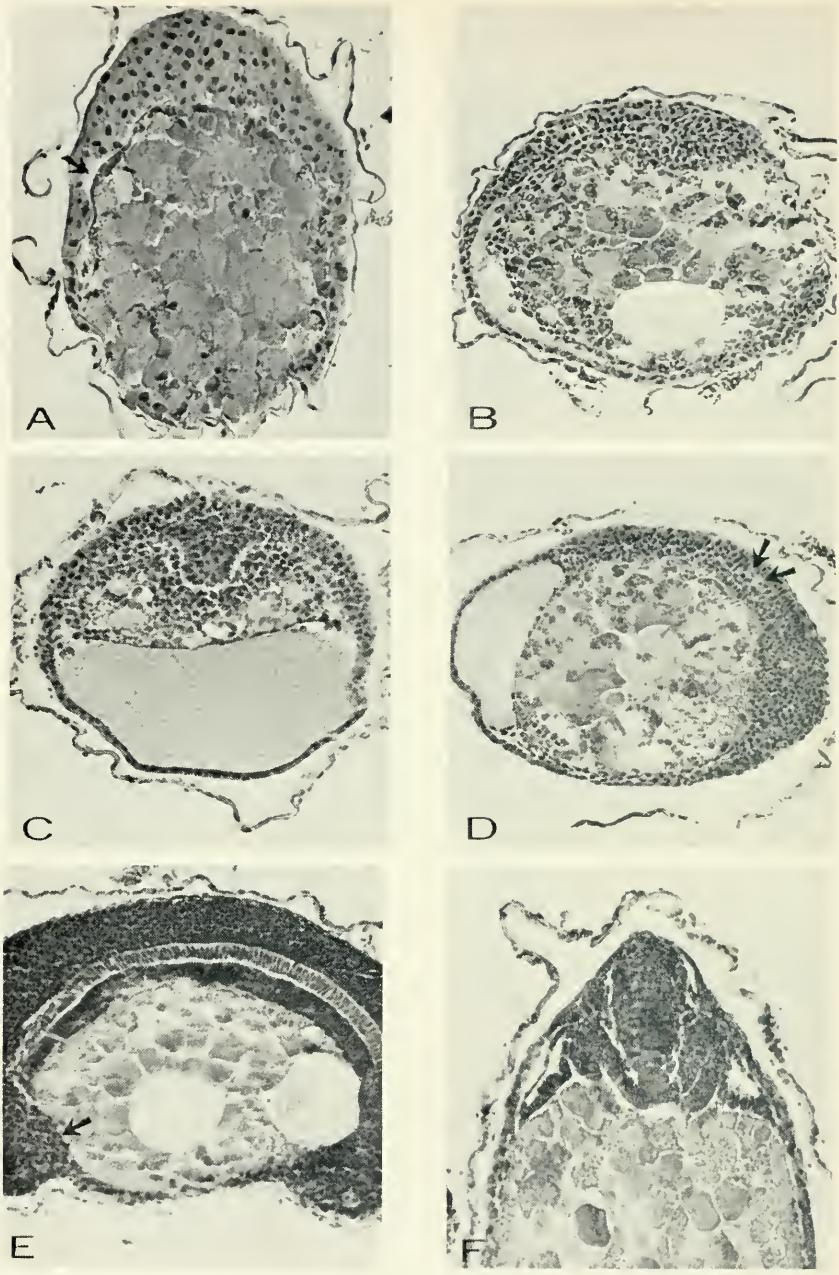

FIGURE 1—A, sagittal section, blastula; the periblast cells are separated from the blastoderm with beginning blastocoele formation (arrow); B, sagittal section, gastrula; the cells of the hypoblast are moving forward from the region of the dorsal lip of the blastopore; the blastopore is still relatively large; C, transverse section, gastrula; this section is from the anterior region and demonstrates a well-developed solid neural keel; the cells of the hypoblast show no differentiation as yet; D, saggital section, gastrula; section lateral to the midline, showing two primitive gonadal cells (arrows); the blastocoele is still a prominent feature; E, median saggital section, 10 somites; the neural keel, notochord, and endoderm are clearly shown; of special interest is the solid mass of cells, the heart primordium (arrow), just rostral to the notochord; F, transverse section, 10 somites; the foregut region, showing the infolding of endoderm to form the alimentary tract.

the newly developing scale, forming a budlike structure in a longitudinal section. As the bony plate elongates from its growth center in the dermis, it carries with it the covering epithelium.

The pectoral and pelvic fins develop as definite outgrowths of dense mesenchymal cells. Pectoral fins are present in 5-mm embryos and the pelvic fins somewhat later in 10-mm specimens. This is in rather marked contrast to the vertical fins, which originate as ectodermal folds containing very few supporting cells. Mesenchymal elements invade these folds later and differentiate to form the ray apparatus.

The tremendous enlargement of the vertical fins during intraovarian life is of special interest in this family of fishes. These fins are well vascularized and the margins between the rays project as small flattened extensions of tissue. This marked increase in the surface area undoubtedly serves a respiratory function and perhaps a nutritional one as well. Shortly before birth, these fins assume their normal size and configuration.

Skeletal System

Following closure of the blastopore and about the time that the somites can be first recognized as separate blocks of tissue, the notochord is visible as a solid cord of cells between the neural keel and the endoderm. The notochord is a very large and prominent structure by the time the embryo has reached 3 mm in length, and continues to be a significant feature throughout the embryonic period.

A thin layer of osteoid substance girdles the notochord at 8 mm, and this is added to continually by the osteoblasts which surround it. In 45-mm specimens just before birth, the central portion is becoming organized and cells occupy the spaces in the central portion as well as at the periphery internal to the bone material surrounding the notochord.

The neural arch, hemal arch, and ribs have a cartilaginous origin. The extensions of the arches surrounding the nerve canal and blood vessels are formed by apposition from a very small cartilaginous center, giving these extensions the same appearance as bone formed by intramembranous ossification.

At 3.5 mm, just caudal to the common cardinal veins, a large mass of relatively undifferentiated cells is found in the lateral walls (Figure 2E). This group of cells is the forerunner of the pectoral girdle. At 5 mm, the pectoral girdle is a conspicuous bar of intramembranously formed bone in the connective tissue on each side of the sinus venosus. The pelvic girdle is derived completely from cartilage bone.

Muscular System

Somite formation is first indicated following closure of the blastopore when about six blocks of tissue can be counted. The cells in these regions rapidly condense to typical somite masses.

Differentiation of the somites to form muscle tissue is seen in the 15-somite embryo when the cells elongate and become acidophilic in their staining reaction. The formation of the myomeres with their connective tissue septa, the myocommata, can be seen in 3.5-mm specimens. They are well visualized at 5 mm, although the trunk musculature is very incompletely formed and present only dorsally.

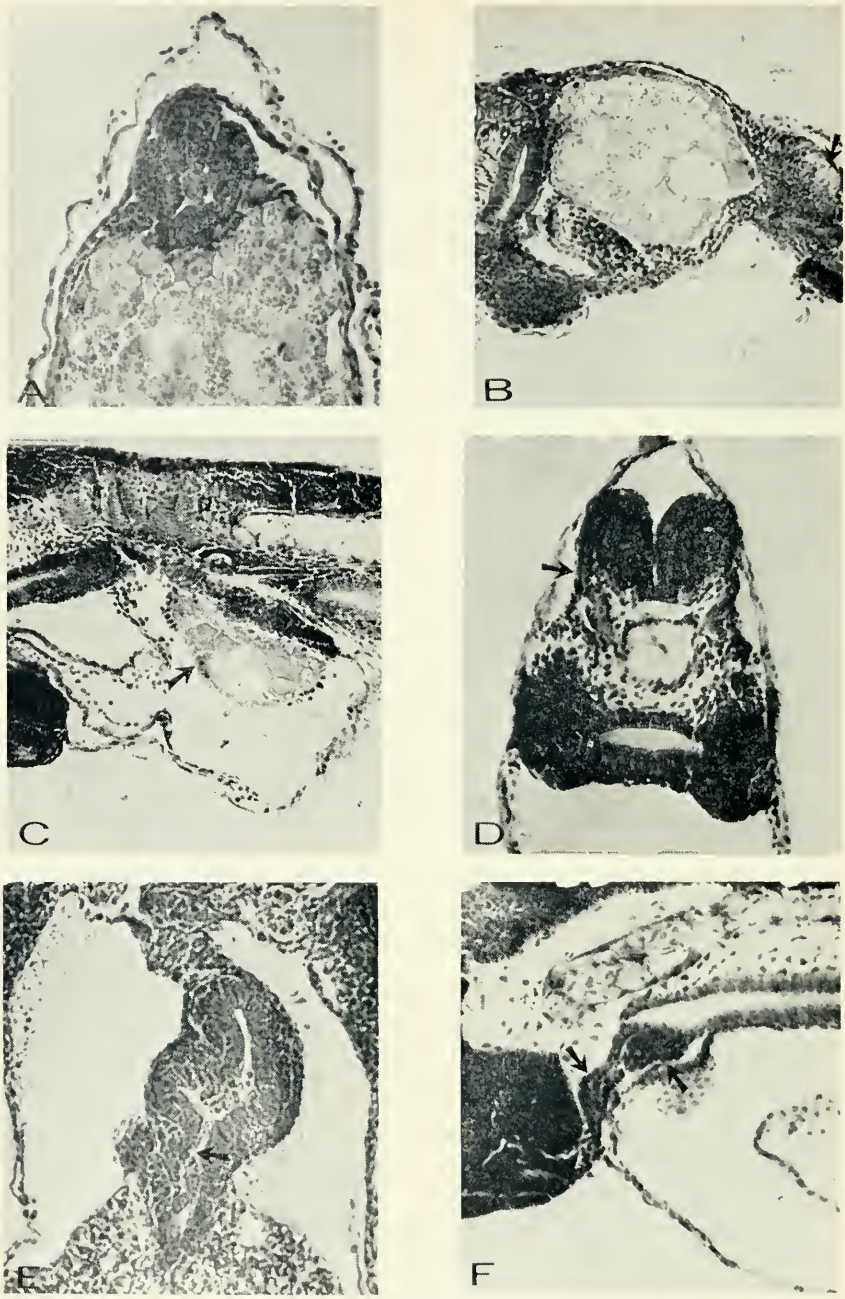

FIGURE 2—A, transverse section, 10 somites; the midgut region in which the ventral layer of cells is oriented at a right angle to the dorsal layer; B, sagittal section, 15 somites; the yolk is still very prominent; a gut lumen is now present; the heart tube is beginning to form and a group of primitive ganadal cells can be seen caudally (arrow); C, sagittal section, 2.5 mm; the yolk is clearly shown in the dorsal region of the sinus venosus in direct contact with the blood; the arrow indicates a periblast cell in the yolk; D, transverse section, 3 mm; section of foregut, showing flagellar-like processes of the columnar cells; neural crest cells are migrating from the dorsolateral region of the neural tube (arrow); E, transverse section, 3.5 mm; the gas bladder diverticulum is dorsal, the gut central, and the liver diverticulum ventral; the pancreatic diverticulum is seen as an outgrowth of the liver diverticulum (arrow); the dense cell masses laterally constitute the primordium of the pectoral girdle; F, sagittal section, 3.5 mm; arrows indicate the pituitary gland forming from the dorsal epithelium of the future mouth cavity and the thyroid gland

The development of the smooth musculature of the intestinal tract occurs relatively late in comparison with skeletal muscle. It was not definitely observed until 8 mm, although at 3.5 mm several layers of undifferentiated mesenchymal cells were forming a layer around the endodermal epithelium.

Alimentary Tract

As the cells of the hypoblast move forward from the region of the dorsal lip of the blastopore during gastrulation, a longitudinal band of cells lying immediately adjacent to the yolk differentiates into endoderm and becomes columnar in shape. Anteriorly in the pharyngeal region, continued multiplication of these cells results in an infolding laterally and a movement medially, forming a double layer of cells which unite to form the most anterior region of the gut (Figure 1F). Caudally, however, the process is not nearly as clear. The cells forming the second layer appear relatively flattened and tend to lie at right angles to the axis of the upper layer (Figure 2A). A lumen soon develops and all of the cells become columnar.

The primary opening of the foregut is through the first gill slit. This opening can be seen in a 15-somite embryo. The anus opens a short time later, probably when the embryo has developed to about the 20-somite stage.

The mouth opening occurs considerably later, when the embryo has grown to about 4 to 4.5 mm in length. Before opening, the future oral cavity consists of a double layer of ectodermal epithelium composed of the ectoderm covering the most rostral part of the brain and the anterior region of the pericardial cavity (Figure 2F). Thus, food material enters by way of the first gill cleft until the mouth opening is established.

This species is equipped with well-developed pharyngeal teeth in addition to those present in the jaws. The pharyngeal teeth can be seen forming in 8- and 10-mm specimens. A dental lamina develops by an ingrowth of the epithelium, causing the mesenchymal cells just beneath to condense in the area and form the dental papilla. The epithelium becomes a two-layered dental organ which in conjunction with the dental pulp, primarily the odontoblasts, is responsible for the outline and formation of the hard structure of the tooth. The teeth of the jaws form in a similar manner but much later.

In the region dorsal to the heart, the cells assume a tall columnar shape and develop long flagellar-like structures (Figure 2D). The apparent function of these structures is to create a current for the movement of food materials. The cells become less prominent at 5 mm and the flagellar-like processes completely disappear by the time the embryo reaches a length of 10 mm. Undoubtedly, swallowing actions and peristaltic movements assume the functions of ingestion and transport of the ovarian secretory products.

By the time the embryo is 5 mm long, the various divisions of the alimentary tract are visible. Histologically, no stomach is present, since the stratified squamous epithelium of the esophagus changes abruptly to the columnar epithelium of the small intestine. There is a definite valve at the junction of the small intestine and the much enlarged hindgut.

The hindgut becomes a rather spectacular structure, enlarging even in the 21-somite stage. The cells become columnar and villi soon develop. These villi become very long and tortuous and appear to fill almost the entire cavity of the hindgut (Figure 3C), which becomes so large that it distorts the normal body outline until shortly before birth.

Liver

The first indication of the liver is seen in the 15-somite embryo as a short diverticulum of the gut with proliferation of cells surrounding it. By the time the embryo has reached 2 mm in length, the organ consists of a rather solid outgrowth of cells located just dorsal to the sinus venosus and the yolk (Figure 2C). At 3.5 mm, the gall bladder and duct system can be identified and at 5 mm it is clearly shown. The liver maintains a very close association with the yolk and eventually envelops it completely.

Pancreas

The pancreas is of the diffuse type, and is extended in a number of directions as rather narrow projections among the associated organs. It also extends along the course of the blood vessels in the liver. It is present in a 3.5-mm embryo as an outgrowth of the common bile duct (Figure 2E), and at 5 mm can be seen definitely as a branch of this duct. At 19 mm, it opens independently but in close association with the bile duct.

Spleen

The spleen begins as a dense aggregation of mesenchymal cells closely associated with the pancreas and liver. While it may be present in 3.5-mm specimens, it was definitely identified when the embryo reached 5 mm in length. It develops into a rather large organ, and just before birth lies lateral to the small intestine, partly enfolded by an extension of the liver.

Respiratory System

Gills have their origin in the branchial arches and can be seen as dense mesenchymal tissue masses between the epithelium forming the pharyngeal pouches. By the time the embryo has grown to 5 mm in length, a bar of cartilage has become well differentiated and the accompanying blood vessel can be observed on the lateral side.

Connective tissue buds develop from the mesenchyme lateral to the cartilage, and each contains a vascular loop and forms a gill filament. As growth continues, each filament develops a cartilaginous core, striated muscle differentiates in the basal region, and many small secondary filaments or lamellae containing capillaries grow out from the surface of the filament.

Gas Bladder

The gas bladder begins as a dorsal diverticulum of the gut just above the hepatic diverticulum (Figure 2E). It is a rather solid mass of cells at first, but a distinct bladder is soon formed. The duct from the bladder to the gut is still apparent in specimens just before birth.

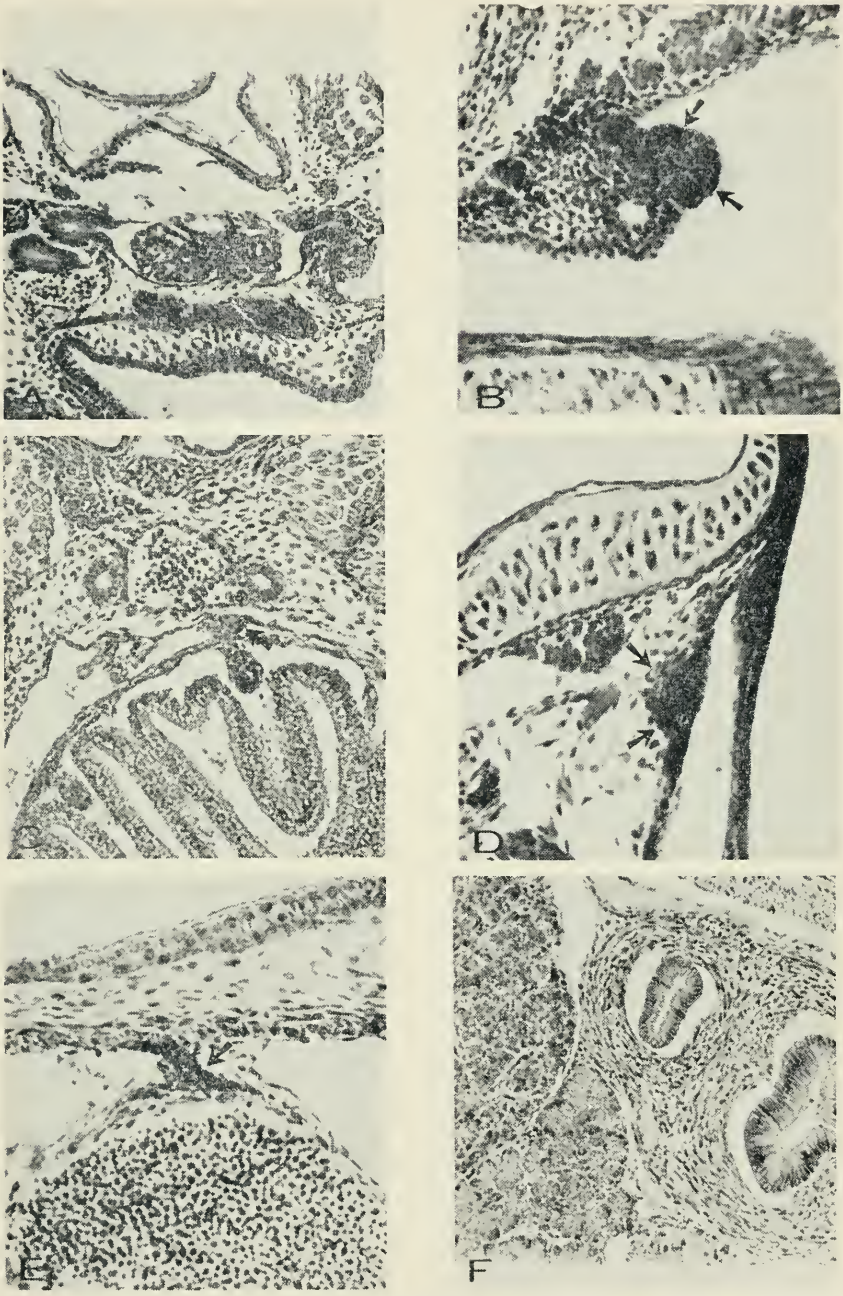

FIGURE 3—A, transverse section, 8 mm; the pronephric units are well developed; the cardinal veins tend to surround the pronephric ducts; B, sagittal section, 8 mm; proliferation of the epithelium in the dorsal evagination of the pharynx, forming the primordium of the epibranchial gland (arrows); C, transverse section, 10 mm; arrow indicates two gonadal cells being surrounded by a mesothelial cell from the peritoneum; D, transverse section, 10 mm; arrows indicate the primordium of the thymus gland as a proliferation of the epithelium in the dorsal medial wall of the branchial chamber; E, sagittal section, 12 mm; the ultimobranchial body is visible as dark-staining cells in the connective tissue between the esophagus and the sinus venosus; F, transverse section, 45 mm; the "principal island" is at the left; compare with pancreatic acini adjacent to it in the lower center region; pancreatic and bile ducts are at the right.

The rete mirabile and gas gland epithelium are relatively late in development. In the most anterior region, the epithelium tends to overgrow the floor and is present in the peripheral parts of the roof. In the most posterior region, the bladder is divided and extends backward as two separate projections. The epithelium completely surrounds these extensions. The rete mirabile is a prominent feature in the connective tissue ventral to the gland epithelium. Branches extend dorsally to ramify among the cells.

The entire dorsal roof remains a very thin structure, with the exceptions noted above.

Excretory System

The first indication of the pronephric element is a dense aggregation of cells in the intermediate plate mesoderm in embryos of about 15 to 20 somites. In the regions dorsal to the yolk and anterior to the liver diverticulum, two renal corpuscles develop in close association with the dorsal aorta. The tubule which leads laterally continues caudally as the pronephric duct. Early formation of these renal corpuscles is well demonstrated in 3-mm embryos and they are well developed by the time the embryo has grown to 8 mm (Figure 3A).

The adult kidney is of the mesonephric type. Beginning tubule formation is noted at 8 mm with the formation of small, dense cell aggregates which subsequently become tubular and can be seen joining the main duct at 12 mm. Glomeruli are also forming in 12-mm specimens. The nephric units are rather small in comparison with the duct size.

In early stages of development, the pronephric duct opens into the caudal end of the hindgut, but as growth proceeds it opens separately just caudal to the anus, the two separate openings being visible at 5 mm.

Reproductive System

The development of the reproductive system is of particular interest because of the early appearance of the primitive gonadal cells. These cells, distinctive and easily identified, are visible in the mesodermal layer during gastrulation (Figure 1D). The cytoplasm is very acidophilic and stains a bright orange with the triosin dye. The nuclear material is evenly dispersed except for the very prominent nucleolus. The nuclear boundary is outlined by a fine dark line in mature cells.

It seems that these cells differentiate at the same time or just before the formation of the primary germ layers. In a serial section of an egg of a related species, *Cymatogaster aggregata*, the shiner perch, the gonadal cells are clearly identified before any differentiation can be seen in any of the other cells.

The majority of these cells soon congregate in the gonadal region (Figure 2B). However, some can be seen in locations far removed from the gonadal area, particularly in the gills. One cell, similar in appearance to the gonadal cells, was noted as a lining cell in the epithelium of the pharynx in a 10-mm specimen. Eigenmann (1892) observed this same phenomenon in *C. aggregata*. Consequently, it is unlikely that these cells are an artifact. It would be of interest to know if the cells have a function in these areas or if they are merely lost.

The gonadal cells migrate from their early position, in the mesenchyme lateral to the notochord, to the peritoneal cavity. In the peri-

toneal cavity they are in contact with the mesothelial lining of the peritoneum, close to the midline on either side of the dorsal mesentery. Mesothelial cells soon envelop them and form the connective tissue covering and mesentery (Figure 3C).

In the female, the two gonads fuse to form a single organ, being separate only at the most anterior end, where a blood vessel enters each horn. The duct opens between the anus and the urinary orifice. The male gonads remain separate with the exception of the ducts, which unite and terminate in conjunction with the urinary opening.

Cardiovascular-yolk Complex

The development in this region is most intriguing because of the marked departure from the normal pattern in those forms developing from telolecithal eggs. The embryo receives nourishment from the mother at a very early stage. Because of this additional food source, the yoke is utilized rather slowly and does not disappear completely until the embryo is at least 10 to 12 mm long.

The earliest indication of the heart is a mass of cells lying just rostral to the notochord and ventral to the most anterior region of the brain. This is well demonstrated in a 10-somite embryo (Figure 1E). At 15 somites the heart lumen is present and the lining cells are differentiating (Figure 2B). When the embryo is at the 21-somite stage, the caudal end of the lumen is approaching the yolk.

The relationship of the yolk and the sinus venosus is clearly shown in the 2.5-mm embryo. By this time, the sinus venosus is a relatively large thin-walled chamber which tends to surround but not cover the yolk (Figure 2C). The yolk projects into the sinus venosus and is in direct contact with the blood circulating through it. It seems probable that in this early stage of development the yolk material is absorbed directly by the blood through the function of the periblast cells in the yolk. By the time the embryo has grown to 5 mm, the transverse septum has developed and separates the pericardial and peritoneal cavities. This division apparently occurs in the region of the early sinus venosus anterior to the yolk, as the yolk now lies in close association with the hepatic vein, which empties into the sinus venosus. This close relationship with the liver and especially the hepatic vein and its larger tributaries is maintained until the final dissolution of the yolk.

The periblast cells associated with the yolk can still be seen in 10- to 12-mm specimens. Their ultimate fate was not determined, although it was thought that periblastic remnants were visible in 16-mm embryos. If this is true, they then degenerate and are absorbed.

Since no vitelline circulation develops and the endothelial cells of the heart appear very similar to the early circulating blood cells, the first blood cells may be derived from this source.

Nervous System

The nervous system development in this species is of the typical teleost type. Differentiation of neural tissue occurs first and becomes a definite entity very early in gastrulation. The neural plate tissue proliferates inward to form a solid cord of cells along the midline. This

solid structure is called the neural keel (Figure 1C). The lumen develops secondarily and is first noted in association with the optic vesicle formation.

The various subdivisions of the brain result from differential growth in the cranial portion of the neural tube and are readily distinguishable in a 10-mm embryo. As development continues, the smaller subdivisions become definite structures and histodifferentiation occurs.

The neural crest cells are conspicuous in the 3-mm embryo. They arise from cells in the dorsal region of the neural tube and migrate ventrally, appearing to move in parallel columns (Figure 2D).

The sympathetic chain is first noted in 10-mm embryos and lies lateral to the dorsal aorta. Some of the cells are heavily pigmented.

Sensory Organs

The first indication of the olfactory organ is the development of nasal placodes in 2-mm embryos. The epithelial cells become columnar in shape as they transform into receptor cells. These cells give rise to the nerve fibers leading to the cerebrum. At 16 mm, the placode is becoming invaginated to form a nasal pit and the nerve fibers are readily observed.

The eye vesicle develops as in any vertebrate by an outgrowth from the diencephalon of the brain. It develops very early and is apparent at about 10 somites and is well developed by 21 somites. The lens develops as a proliferation of the basal epithelium superficial to the eye vesicle.

The ear also develops by an ingrowth of the basal epithelium. The cavity develops secondarily, and initiation can be seen in a 10-somite embryo. By the time the embryo has reached 5 mm, the subdivisions are being formed by the modification of the original otocyst and the sensory epithelium is beginning to differentiate by becoming columnar in shape. At 19 mm, the otoliths are visible, and are the result of calcium deposition in the substance of the ear chamber.

The sensory cells of the lateral line system are first noted at 10 mm. These are present first in the most anterior region of the lower jaw. As is common to most systems, development proceeds in a caudal direction. The neuromasts develop in a manner similar to the development of the olfactory organ. The epithelial cells differentiate, becoming columnar in shape. The canal system develops by the formation of a groove and the fusion of the epithelium of its margins.

Endocrine System

The origin of the pituitary gland can be seen as a solid proliferation of cells in the roof of the ectodermal invagination which will form the mouth cavity. This can be observed in 3- to 4-mm specimens (Figure 2F). In embryos 5 mm in length, the gland is a distinct structure lying beneath the saccus vasculosus.

The pineal develops as an evagination in the roof of the brain, just rostral to the developing optic lobes. This outgrowth is visible in 10-mm specimens.

The primordium of the thyroid develops very early, being perceptible in 15-somite embryos as a solid downgrowth from the most anterior

region of the foregut (Figure 2F). As development continues, it becomes associated with the ventral aorta and its branches. Its histological picture becomes characteristic of thyroid tissue in general and is well developed before birth.

The thymus develops relatively late, being perceptible in 10-mm embryos as an inward proliferation of the epithelial cells on the posterior superior medial wall of the branchial cavity (Figure 3D). By this time, the branchial pouches have disappeared completely as embryological structures. Consequently, there appears to be no direct relationship between the origin of this gland and the epithelium of any of the pouches. It becomes infiltrated with lymphocytes and continues to maintain its superficial position, being covered externally only by the epithelial layer.

The ultimobranchial body consists first of a small group of cells in the connective tissue between the esophagus and the sinus venosus. These cells are first identified with any degree of certainty in 10-mm specimens and are readily distinguishable at 12 mm (Figure 3E). The origin of these cells could not be determined, but they probably arose from the last pharyngeal pouches (Gorbman and Bern, 1962). Before birth, a number of small blood vessels are present among the cell groupings, providing evidence for an endocrine function.

In this fish, the pancreatic islet tissue is concentrated into a definite single structure, the principal island, just lateral to the bile and pancreatic ducts (Figure 3F). It is first clearly visible in 12-mm specimens as an aggregation of cells which is distinctive and readily differentiated from the cells forming the pancreatic acini.

Both the interrenal and chromaffin cells are closely associated with the cardinal veins in the cranial region of the kidney. Interrenal cells can be observed differentiating in 12-mm embryos and are a prominent feature before birth. The cells are present as cords and sheets, but always close to a vein. The presumed chromaffin cells are not well shown even in 45-mm embryos, but appear immediately adjacent to the cardinal veins as fairly large cells with very pale cytoplasm.

The epibranchial or pseudobranchial gland is located in a transverse cleft in the anterior roof of the pharynx. In adult fish, it has the gross appearance of a miniature gill. Embryologically, it has its origin in the dorsal portion of the anterior wall of a transverse vertical evagination of the roof of the pharynx, just anterior to the pharyngeal teeth. It begins as an epithelial proliferation in 8-mm embryos (Figure 3B). The cells become very acidophilic and are arranged in cords supported by a connective tissue and cartilage stroma.

Two gland-like structures, the corpuscles of Stannius, are present in specimens just prior to birth. They develop in the caudal kidney region just above and posterior to the junction of the mesonephric ducts. It was difficult to learn much about their origin because they appeared so similar to the developing kidney tubules. However, in one specimen, duct structure was identified in the corpuscle as well as associated with the mesonephric duct, but continuity between the two was lost. Corpuscles of Stannius remain as solid structures and histologically appear to be modified kidney tubules.

DISCUSSION

In comparing the development of *H. argenteum* with other teleost fishes, major differences are present in the very early stages of growth in both the digestive and cardiovascular systems. These modifications are primarily concerned with nutrition until the mouth and the alimentary tract have developed sufficiently to perform their functions in the normal way.

The yolk, although extremely small, is utilized quite slowly. It is not completely absorbed until the embryo has attained a length of about 12 mm. For all practical purposes the yolk lies within the sinus venosus. Consequently, a vitelline circulation is absent and absorption of the yolk is directly into the blood circulating through the heart. A small number of periblast cells are present in the yolk, and they probably have the function of reducing the yolk substance to a soluble form which can be carried by the blood and utilized by the body.

Even before hatching, the mechanism for food intake is quite well developed. This mechanism seems to be unique to the Embiotocidae, and makes it possible for the embryos to ingest the ovarian secretory products soon after hatching. Evidence which supports the use of the ovarian secretions as food is the small size of the yolk, which could not support a long growth period, the modifications in the alimentary tract, and the presence of ovarian cellular material in the digestive tract.

In addition to the specialized structures for nutrition, modifications for respiration are present. In the early stages of development, gas exchange must occur through the epithelial surfaces of the body. Later, as the vertical fins develop, the surface area greatly increases because these fins become much elongated and even possess small tissue extensions between the fin rays. These fins are extremely well vascularized, a fact which is clearly demonstrated by their pronounced red color.

The long gestation period permits the young to develop to a considerable size before birth. In this particular species, unborn specimens which were 45 mm in length were obtained. Since relatively few young are produced by each female, a large size at birth is of definite survival value to the species.

CONCLUSIONS

1) Development appears to be typical of teleost fishes with the exception of the digestive and cardiovascular systems. The differences in these two systems represent nutritional modification in the very early stages of growth.

2) The early kidney consists of two well-developed renal corpuscles. Later, the adult mesonephric kidney forms and these early corpuscles lose their significance.

3) Primitive gonadal cells are first seen during gastrulation as large acidophilic cells in the mesoderm. These observations support the view that these cells differentiate before or at the same time that the primary germ layers are becoming established.

4) The thymus gland begins as an epithelial ingrowth from the medial wall of the branchial chamber, and no direct relationship can be seen between its origin and any of the branchial pouches. The thymus maintains a very superficial position in the dorsal region of the medial wall of the branchial chamber.

5) Pancreatic endocrine tissue is concentrated into one large principal island.

6) The epibranchial gland begins as an epithelial proliferation in a transverse cleft in the roof of the pharynx. In later embryos, it consists of acidophilic cells supported by a cartilage and connective tissue stroma.

7) The corpuscles of Stannius appear to be formed as a result of an outgrowth of the mesonephric duct since in one specimen a duct could be clearly seen in one of the corpuscles. Whether they were formed by the proliferation of cells of the duct or from differentiation of cells in the mesenchyme was not determined.

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RECORDS OF SOME NATIVE FRESHWATER FISHES TRANSPLANTED INTO VARIOUS WATERS OF CALIFORNIA, BAJA CALIFORNIA, AND NEVADA[1]

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Records of transplants of certain cyprinids, catostomids, and cyprinodontids made between 1939 and 1955 are described. All records are given whether or not they were successful. The purpose was to test the effects of changed environment on meristic and morphometric characters. The waters involved are located in southern California, southern Nevada, and northern Baja California. Successfully established at the present time as a result of this work are populations of *Rhinichthys osculus*, *Cyprinodon nevadensis amargosae*, and *Cyprinodon salinus*.

INTRODUCTION

Nearly 30 years ago I began some transplantation experiments with native freshwater fishes of California, mostly of the genus *Cyprinodon*, designed to test the effects of changed environment on meristic and and morphometric characters (Miller, 1948: 111–126). No record of these transplants has heretofore been published (although typed lists were distributed to a few ichthyologists) and, since some were successful, the data should be made available lest zoogeographers and others be led astray. All attempts to establish species are discussed, whether they failed or not. A summary of the transplants is given in Table 1.

RESULTS

Gila orcuttii (Eigenmann and Eigenmann)—arroyo chub

This species is native to coastal streams of southern California from Malibu Creek, in extreme southwestern Los Angeles County, southward to the basin of San Luis Rey River, Riverside County. Its occurrence in the Santa Clara-Ventura river systems and in the Santa Ynez River basin, north of Los Angeles and Santa Barbara, respectively, very probably represents introductions. To my knowledge the species was first collected in the Santa Clara in 1934 and in the other two drainages in 1940 (see also discussion of distribution of *Rhinichthys osculus* in Miller, 1946*b*: 207). It is also now abundant in Gaviota Creek, Santa Barbara County (D. W. Greenfield, pers. comm., 1967).

On April 3, 1950, 60 half-grown to large adult individuals were planted in excellent condition in the lower part of Sentenac Canyon, in San Felipe Creek, a western flood tributary of the Salton Sea about 12 miles east of Julian, San Diego County. These fish had been collected the same day in Temecula Creek (tributary to Santa Margarita River) at Oak Grove, north of Lake Henshaw, San Diego County.

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When the canyon was revisited on June 14, 1950, only *Gila mohavensis* was collected (see below). Subsequently, this area of the creek became dry and only dead fish (no *Gila orcuttii*) were found (observation of C. L. Hubbs, April 1959).

On May 6, 1955, 50 individuals of various sizes were stocked in Río Santo Tomás, Baja California del Norte, at the first crossing below the highway at the upper end of the canyon. This locality lies approximately 20 airline miles south of Ensenada, at about 31° 35′, 116° 32′. These fish had been collected from the San Luis Rey River just west of Warner Hot Springs, San Diego County, on May 3. During his frequent trips to Baja California del Norte, Carl L. Hubbs failed to find any evidence of establishment of this species or *Gila mohavensis* (see below) in Río Santo Tomás.

Gila (*Siphateles*) *mohavensis* (Snyder)—Mohave chub

The allocation of *Siphateles* as a subgenus of *Gila* stems in large part from research by Uyeno (unpublished doctoral thesis, 1960, University of Michigan). Species assigned to *Siphateles* commonly hybridize where they are sympatric with *Gila* (*sensu stricto*), the osteology of the two subgenera is remarkably alike, and *Siphateles bicolor obesus*, of the Lahontan basin, is so similar to *Gila atraria* that the two taxa can only be distinguished by removing the pharyngeal teeth (uniserial in *Siphateles*, biserial in *Gila*). It is obvious that the two groups are intimately related, that *Siphateles* is derived from *Gila*, and that genes of *Gila orcuttii* have infiltrated those of *Siphateles mohavensis* (and vice versa) in the Mohave River basin to the extent that resulting samples are now (1967) difficult to assign to species. This introgressive hybridization is currently under experimental study by David W. Greenfield (California State College, Fullerton); a paper summarizing the hybridization history in the Mohave River, based on morphology, is in preparation by Hubbs and Miller (see also Hubbs and Miller, 1943).

On May 23, 1939, 48 individuals were introduced into the deep pool of San Felipe Creek below the highway bridge in Sentenac Canyon, San Diego County. These fish had been collected on May 20, 1939, in the concrete, spring-fed pool on the west side of Soda (Dry) Lake, south of Baker, San Bernardino County (at what has been known as Zzyzx Mineral Springs Resort). On June 8, 1939, no chubs were noted. About 110 fish (3 to 4 inches long) from this same place were stocked in Sentenac Canyon on July 29, 1940, at which time many young of the previous year's transplant were seen, indicating successful reproduction. On June 29, 1941, the canyon was checked by Ralph G. Miller and the pool just above the bridge was teeming with fish of all age groups. On March 23, 1942, W. I. Follett saw many fish in the canyon. On July 25, 1945, R. G. Miller again visited the canyon and found changes in the pool below the original bridge, which resulted from impending widening and straightening of State Highway 78. Fish were common, however, above the old bridge and 77 were preserved. On May 2, 1948, 483 individuals were preserved for comparison with the original stock at Soda Lake. By this time the original bridge had been replaced and the "old bridge hole" was destroyed. On June 14, 1950, young were collected for the same purpose. On May 3, 1955, fish were

TABLE 1

Transplant Records of Some Californian Fishes, 1939–1955

Taxon	Date	Origin	Where transplanted	Results	Remarks
Gila orcuttii	IV:3:1950	Temecula Cr., San Diego Co.	San Felipe Cr., San Diego Co.	Negative	None found VI:14:1950
Gila orcuttii	V:6:1955	San Luis Rey R., San Diego Co.	Río Santo Tomas, Baja California	Negative	See text
Gila (Siphateles) mohavensis	V:23:1939 VII:29:1940	Soda L., San Bernardino Co.	San Felipe Cr., San Diego Co.	Positive; negative	Successful for 20 years, then gone; see text
Gila (Siphateles) mohavensis	V:6:1955	Soda L., San Bernardino Co.	Río Santo Tomas, Baja California	Negative	See text
Rhinichthys osculus	V:29:1939	Little L., Owens Valley, Inyo Co.	Willow Cr., Saline Valley, Inyo Co.	Negative	Inadequate habitat
Rhinichthys osculus	VIII:31:1940	San Gabriel R., Los Angeles Co.	River Sprs., Adobe Valley, Mono Co.	**Positive**	Common in 1965
Rhinichthys osculus	V:18:1940	Shoshone Spr., Inyo Co.	Old Borax Works, Death Valley	Negative	No water X:2:1940
Catostomus (Pantosteus) santaanae	VIII:31:1940	San Gabriel R., Los Angeles Co.	River Sprs., Adobe Valley, Mono Co.	Negative	None seen 1941; none seen or collected 1965
Cyprinodon macularius	V:24:1939	Carrizo Cr., Salton Sea basin, Imperial Co.	Dos Palmas, NE side, Salton Sea (accidental release), Riverside Co.	Negative, probably	See text
Cyprinodon macularius	VIII:2, 9:1940	Date Palm Beach, Salton Sea, Riverside Co.	Spr. at Little L., Owens Valley, Inyo Co.	Negative	See text
Cyprinodon nevadensis					
C. n. nevadensis	X:27:1939 IX:6:1940	Saratoga Sprs., Death Valley, San Bernardino Co.	Lucerne Valley reservoir, San Bernardino Co.	Negative	None seined in 1940 or 1941; fish lost when reservoir cleaned by rancher
C. n. amargosae	V:18:1939 VIII:3:1940	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	Spr. at Little L., Owens Valley, Inyo Co.	Negative	None seen 1940; none seen or seined 1942
C. n. amargosae	V:24:1939 VII:29:1940	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	Shoreline Spr., Salton Sea, Riverside Co.	Negative	No open water in spring 1941

TABLE 1—Continued

Transplant Records of Some Californian Fishes, 1939–1955

Taxon	Date	Origin	Where transplanted	Results	Remarks
C. n. amargosae	VI:8:1939	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	San Felipe Cr., San Diego Co.	Negative	See text
C. n. amargosae	VIII:4:1940	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	Pahrump Ranch, Nye Co., Nev.	Negative	Gone by 1941
C. n. amargosae	VIII:30:1940	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	River Sprs., Adobe Valley, Mono Co.	Positive	Abundant in 1965
C. n. amargosae	VIII:30:1940, IX:1:1940	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	Outlet, Little L., Owens Valley, Inyo Co.	Negative	None seen 1940; none seen or collected 1942
C. n. amargosae	VI:13:1941	NW of Saratoga Sprs., Death Valley, San Bernardino Co.	Lucerne Valley reservoir, San Bernardino Co.	Negative	Survived through 1942; see text
C. n. shoshone	V:18:1939	Shoshone Spr., Inyo Co.	Old Borax Works, Death Valley, Inyo Co.	Negative	No water X:2:1940
Cyprinodon salinus	I:11:1939, V:20:1939, VIII:4:1940	Salt Cr., Death Valley, Inyo Co.	Pool at Soda L., San Bernardino Co.	Positive	Abundant by 1955
Cyprinodon salinus	V:19:1939, VIII:3:1940, IX:1:1940	Salt Cr., Death Valley, Inyo Co.	Deep Sprs. Valley, Inyo Co.	Negative	Survived at least until IX:2: 1942; none found 1967
Cyprinodon salinus	VIII:3:1940	Salt Cr., Death Valley, Inyo Co.	Near Fish Sprs., Owens Valley, Inyo Co.	Negative	No fish seen 1941
Cyprinodon salinus	VIII:31:1940	Salt Cr., Death Valley, Inyo Co.	River Sprs., Adobe Valley, Mono Co.	Positive	Abundant in 1965

numerous. On April 3, 1959, R. R. Miller and R. J. Schultz saw no fish but good pools in the lower part of the canyon. Later in April 1959, as recounted above under *Gila orcuttii*, only dead fish were observed by C. L. Hubbs when the creek had become nearly dry. Remains of hundreds were found in one small remaining pool. Thus, after 20 years, the erstwhile successful introduction had failed.

On May 6, 1955, 27 individuals from Soda Lake were introduced in Río Santo Tomás, Baja California del Norte, as recounted above for *Gila orcuttii*. The objective of this experiment was to observe if a hybrid swarm would develop from these two species, as in the Mohave River. Unfortunately, neither became established.

Rhinichthys osculus (Girard)—speckled dace

In coastal streams of southern California, this otherwise ubiquitous fish seems to be native only to the Santa Ana River system (Culver and Hubbs, 1917), which includes all of the drainage of the Los Angeles Plain. Although it has been recorded from the Santa Clara River basin, just north of Los Angeles, and from tributaries of the Cuyama River in southern San Luis Obispo County (Miller, 1946*b*: 207), the populations there almost surely represent introductions. This idea is strengthened, for the Cuyama River record, by the occurrence at the same station of the Monterey western roach, *Hesperoleucus symmetricus subditus* (Miller, 1946*a*: 197), collected in 1940. North of the Santa Ana system, on the Pacific slope, *R. osculus* is evidently native to San Luis Obispo Creek (Jordan, 1894), San Luis Obispo County, and to other coastal streams northward from that point. Thus, there apparently was a real hiatus in its natural distribution between the Los Angeles Plain and San Luis Obispo Creek.

In the interior drainage of the Death Valley system (Miller, 1948), the speckled dace occurs only in the Owens and Amargosa river basins.

On May 29, 1939, 32 individuals were introduced into Willow Creek, near the northwestern end of Saline Valley, about 17 airline miles due east of Independence, Inyo County, California. These fish had been collected the previous day from the spring-fed outlet of Little Lake, just below the hotel at Little Lake, in southern Owens Valley. When Willow Creek was carefully checked on June 28, 1967, no fish were found. There was obvious evidence of the powerful scouring effects of flash floods along the creek, which thus render the habitat inhospitable to fish life.

On August 31, 1940, 143 individuals were introduced into River Springs, on the east side of Adobe Valley, T. 1 N., R. 30 E., sec. 24, Mono County, California. These fish had been collected on August 28 from the San Gabriel River near the Montebello Oil Fields just northwest of Whittier, Los Angeles County. On September 10, 1941, when the transplant was checked by R. G. Miller, no fish were seen. However, on August 16, 1967, speckled dace were common at River Springs.

The successful establishment of this distinctive stock is fortunate, since no native fishes whatever now occur in the San Gabriel River or elsewhere on the Los Angeles Plain.

On May 18, 1940, about 10 individuals of this species were transferred from the outlet of Shoshone Spring at Shoshone, Inyo County, to the

Old (Eagle) Borax Works on the west side of Death Valley. When revisited on October 2, 1940, the water had disappeared.

Catostomus (Pantosteus) santaanae (Snyder)—Santa Ana mountain-sucker

The relegation of *Pantosteus* as a subgenus of *Catostomus* is dealt with by Smith (1966: 42–46).

This species is known from the Santa Clara, Los Angeles, San Gabriel, and Santa Ana rivers of southern California, but it is probably not native to the Santa Clara. An old resident of that drainage testified that the only fish present originally in the Santa Clara system was a small species, about 2 to 3 inches long, that swam in a jerky fashion and curled its tail when at rest. This obviously refers to *Gasterosteus aculeatus* (Hubbs, pers. comm.).

On August 31, 1940, 2 individuals of this sucker were accidentally introduced into River Springs, Adobe Valley (see above, under *Rhinichthys osculus*; they had also been collected from the same locality as was that species). When the springs were examined on September 10, 1941, no suckers were seen, and none was collected during the thorough survey of Adobe Valley on August 16–17, 1965.

Cyprinodon macularius Baird and Girard—desert pupfish

The distribution of this species was treated by Miller (1943). It lives today only in the Salton Sea basin of southeastern California, in one or two localities in Arizona, and in the Sonoyta Creek drainage, along the Arizona-Sonora line.

On May 24, 1939, at least six individuals escaped from a trap into Dos Palmas Spring, which lies near the northeastern corner of the Salton Sea, less than a mile south of the Coachella Canal (built since 1939). These fish had been collected the same day near the southwestern end of the Salton Sea from Carrizo Creek near its junction with San Felipe Creek, Imperial County. When the spring was revisited by R. G. Miller on February 4, 1940, no fish were seen, but on July 29, 1940, one fish was observed. On March 12, 1950, Kenneth S. Norris collected three individuals (25 to 34 mm SL) in Dos Palmas Spring, along with nine adults of *Gambusia a. affinis*. Whether these pupfish represent the stock introduced from Carrizo Creek is not certain, especially in view of the appearance of mosquitofish in Dos Palmas Spring between 1940 and 1950. A large collection would need to be preserved for comparison with the Carrizo Creek population, but even then the identity of the stock might remain in doubt.

On August 2 and 9, 1940, 53 specimens of desert pupfish were introduced into the most southeasterly of the head springs feeding the ditches at Little Lake in southern Owens Valley. These fish were collected on July 29 in the Salton Sea at Date Palm Beach, at the northeastern corner of the Sea about 8 miles south of Mecca. A few minutes after introduction the fish swam about with their heads out of water breathing rapidly, perhaps due to high CO_2 tension. On August 30, 1940, not one fish was found.

Cyprinodon nevadensis Eigenmann and Eigenmann—Nevada pupfish

Three subspecies of this pupfish, as delimited by Miller (1948), were transplanted as follows:

C. n. nevadensis.—This subspecies is confined to Saratoga Springs (80 to 85 F) in the southeastern arm of Death Valley. On October 27, 1939, R. G. Miller introduced 90 individuals into the reservoir on a ranch (owned by Roy Kendall) in Lucerne Valley, San Bernardino County. Fish were seen there on December 16, 1939, and, despite the formation of a thin layer of ice during the winter, 30 young were recovered by the rancher when he drained the pond early in the spring of 1940. When the reservoir was seined on July 11, 1940, however, we were unable to find any pupfish. Therefore, on September 6, 1940, 96 more individuals were stocked. A sizable population of pumpkinseed sunfish (*Lepomis gibbosus*) was observed at this time. On April 27, 1941, R. G. Miller was unable to seine any pupfish. He learned that a tenant (the rancher died in September 1940) had drained the pool 3 weeks earlier but saw few fish. This transplant failed when the pond was drained.

C. n. amargosae.—This subspecies occurs in the Amargosa River in California (in Death Valley, and near and below Tecopa). Only the Death Valley race was used for transplants (see Miller, 1948: 29). On May 18, 1939, about 150 fish were placed in the head warm spring at Little Lake, Owens Valley. No fish were seen in the spring or ditches on August 2, 1940. On August 30, 1940, 50 more were introduced, and on September 3, 1942, a thorough seining yielded no specimens. The transplant evidently failed for the reason hypothesized under the account of *Cyprinodon macularius.*

On May 24, 1939, 110 fish were put into "Shoreline Spring," near the northeastern end of Salton Sea only 0.7 mile from Dos Palmas Spring, Riverside County. They had been collected in Death Valley on May 20. After a few hours nearly all the fish were observed at the surface. On February 4, 1940, no fish were seen in the spring by R. G. Miller. On July 29, 1940, 200 additional fish of all sizes were introduced, and on August 7, 1940, at least 25 or 30 fish could be seen at one time. On October 23, 1940, R. G. Miller could find no fish although the spring was very clear. Finally, on June 29, 1941, Shoreline Spring contained no surface water at all, and the former pool had become completely overgrown by dense stands of tules. No fish could be seen.

On June 8, 1939, 114 individuals (mostly young) were placed in San Felipe Creek, in Sentenac Canyon, directly under the old highway bridge. These had been collected on June 4. No pupfish were seen in the creek on July 29, 1940, or on subsequent visits.

On August 4, 1940, about 750 pupfish of all sizes which had been collected 4 hours earlier in Death Valley, were placed in the head spring at Pahrump Ranch, Pahrump Valley, Nye County, Nevada. A thorough check on June 12, 1941, by R. G. Miller, failed to reveal any individuals in the clear spring pool which, as in 1940, contained *Empetrichthys latos* and carp.

On August 30, 1940, approximately 350 fish of all sizes were planted in River Springs, Adobe Valley, Mono County (see account of

Rhinichthys osculus). Although none was seen by R. G. Miller on September 10, 1941, pupfish were common there on August 16, 1965.

Also on August 30, 1940, about 400 pupfish of all sizes (taken the same day in Death Valley) were placed in spring-fed ditches about 300 yards below the hotel at Little Lake, Owens Valley. Although they showed no distress, and hundreds were seen here on September 1, 1940 (when 58 additional individuals were stocked), only 8 days later none was observed during 2 hours of searching. On September 3, 1942, the habitat was thoroughly seined and yielded no pupfish, and none was seen on subsequent visits. Possibly these fish were eaten by largemouth bass.

On June 13, 1941, about 100 individuals were carried from Death Valley to the reservoir in Lucerne Valley, San Bernardino County (see account of *C. n. nevadensis*), where they were stocked by R. G. Miller and observed for about 3 hours. They seemed perfectly at home. When again checked on August 15, 1941, they were in fine condition, with many newborn young. Again, on November 17, 1941, many young and adults were seen and on June 3, 1942, fish were abundant. On September 24, 1942, the pond was seined thoroughly and fish of varied sizes were found. No further checks were made, but the stock doubtless died out when the reservoir was drained or destroyed.

Cyprinodon n. shoshone.—This subspecies is known only from Shoshone Warm Spring and its outlet near Shoshone, Inyo County. On May 18, 1939, well over 100 individuals were placed in the Old (Eagle) Borax Works on the west side of Death Valley. By October 2, 1940, no water remained in this locality.

Cyprinodon salinus Miller—Salt Creek pupfish

This species occurs in Salt Creek, on the floor of Death Valley east of Stovepipe Wells, and in briny pools on the valley floor farther south in "Pupfish" (= Cottonball) Marsh—see Hunt et al. (1966: 35).

About 150 individuals, mostly young, were collected on January 10, 1939, and introduced the next day into the spring-fed pool at Soda Station, on the west side of Soda (Dry) Lake south of Baker, San Bernardino County, California. On April 8, 1939, about 6 individuals were observed. On May 20, 1939, an additional 140 were stocked after first seining from the pool 2 females of the previous transfer. On June 3, 1939, at least 60 individuals were observed in the pool, but on October 22, 1939, R. G. Miller could see no pupfish after a 45-minute search. Aquatic vegetation may have hidden them, however.

On July 28, 1940, a pair was observed after spending 1½ hours cleaning the pool of thick vegetation with a rake. On August 4, about 400 more pupfish were stocked and 1 female from former transfers was caught when seining the pool. On August 30, many young and adults (estimated by R. G. Miller to total at least 200) were seen.

On July 12, 1941, only 1 pupfish (a male) was seen by R. G. Miller in a half-hour search, but on May 1, 1955, the species was common and has been ever since (last checked on July 5, 1967), although during winter (as on January 3, 1966) it is difficult to observe individuals. This is one of only two transfers of *Cyprinodon* that have proved successful.

On May 19, 1939, over 120 Salt Creek pupfish were introduced into spring-fed ditches of Deep Springs Valley, east of Bishop in northern Inyo County. The fish had been collected the previous day and held overnight in a trap at Little Lake. The introduction was made just southwest of the old stone corral. The fish were in excellent condition and responded well to the new habitat. Returning on August 3, 1940, the ditches were thoroughly searched but no pupfish could be found. On this date, more than 400 additional fish (mostly young) were stocked and these, too, responded well. On August 15, 1940, 7 young to adult specimens were collected by D. D. McLean and H. M. Bourland and sent alive to George S. Myers. On September 1, 1940, only 3 fish were seen or captured after a long search, but heavy plant cover and the large number of ditches made seining difficult. An additional 26 pupfish, not in very good condition, were stocked. On September 2, 1942, 1 pupfish was seen. A very careful search of the ditches (including seining) by 10 persons on July 27, 1967, revealed only carp.

On August 3, 1940, over 300 Salt Creek pupfish (mostly young-of-the-year) were transplanted to one of the spring sources of the slough at Fish Springs, about 6 miles south of Big Pine in Owens Valley, Inyo County. The pool where they were introduced was about 40 feet in diameter, with much duckweed on the surface (over half of which was removed prior to stocking so that fish could be more easily observed). On September 1, 1940, no fish were seen (overcast day), and the spring was cleared of excess algae. On September 9, 1941, the spring was entirely covered with a crust of vegetation so thick it was difficult to penetrate with a stick. A surface hole 6 feet in diameter was excavated directly over the spring source where the water was 3 to 4 feet deep. Though the water was very clear, no fish could be seen.

On August 31, 1940, over 425 pupfish were put into the main spring pool at River Springs, Adobe Valley (see account of *Cyprinodon nevadensis amargosae*). On September 10, 1941, R. G. Miller was unable to see a single pupfish in the clear water of the spring or in any of the outlet ditches. However, on August 16, 1965, pupfish were abundant.

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THE AQUATIC OLIGOCHAETA OF THE SAN FRANCISCO BAY SYSTEM[1]

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The aquatic Oligochaeta in samples of the bottom-dwelling organisms from the San Francisco Bay system have been identified, and their distribution and relative abundance considered in relation to the chemical and physical properties of the water and the sediment. The predominantly saltwater area is inhabited by three marine tubificids, *Peloscolex gabriellae*, *P. apectinatus*, and *P. nerthoides*. In the area exposed to the greatest inflow of fresh water, different species predominate, but there are few worms in the region which is subject to the widest range of salinities. Gross organic pollution reduces the numbers of all organisms present and also reduces the diversity of the fauna so that even a small number of oligochaetes may represent 100% of the fauna. Where large amounts of organic matter are present, but the oxygen concentration is not too drastically reduced, the number of bacteria is very high and there is a parallel increase in the abundance of worms. In areas where industrial pollutants are known to enter the bay, the number of worms is reduced.

INTRODUCTION

The oligochaete material on which this report is based was collected during the 1961–62 year of the Comprehensive Study of San Francisco Bay carried out for the State Water Pollution Control Board[2] by the Sanitary Engineering Research Laboratory of the College of Engineering and School of Public Health of the University of California, Berkeley.

Data on many aspects of this study have been published in a series of reports, those for the fiscal year 1961–62 (Storrs, Selleck, and Pearson, 1963) relating immediately to the material available. Extensive use of these published data has been made in an attempt to explain the observed distribution of aquatic oligochaetes.

THE AREA STUDIED

East of the Golden Gate, the bay extends a considerable distance north and south of a line between San Francisco and Oakland. To the south lies the South San Francisco Bay area, which receives some fresh water from Coyote Creek and other tributaries but is predominantly a saltwater or brackish region. Sampling in this area was restricted to the portion south of the San Mateo-Hayward Bridge. With the exception of stations 1 and 2, the sampling sites form a linear series (Figure 1). The sampling stations also form a linear series in Suisun Bay, which is formed by the confluence of the Sacramento and San Joaquin

[1] Submitted for publication March 1967.
[2] Later the State Water Quality Control Board, which now has been merged with the State Water Rights Board into the new State Water Resources Control Board.

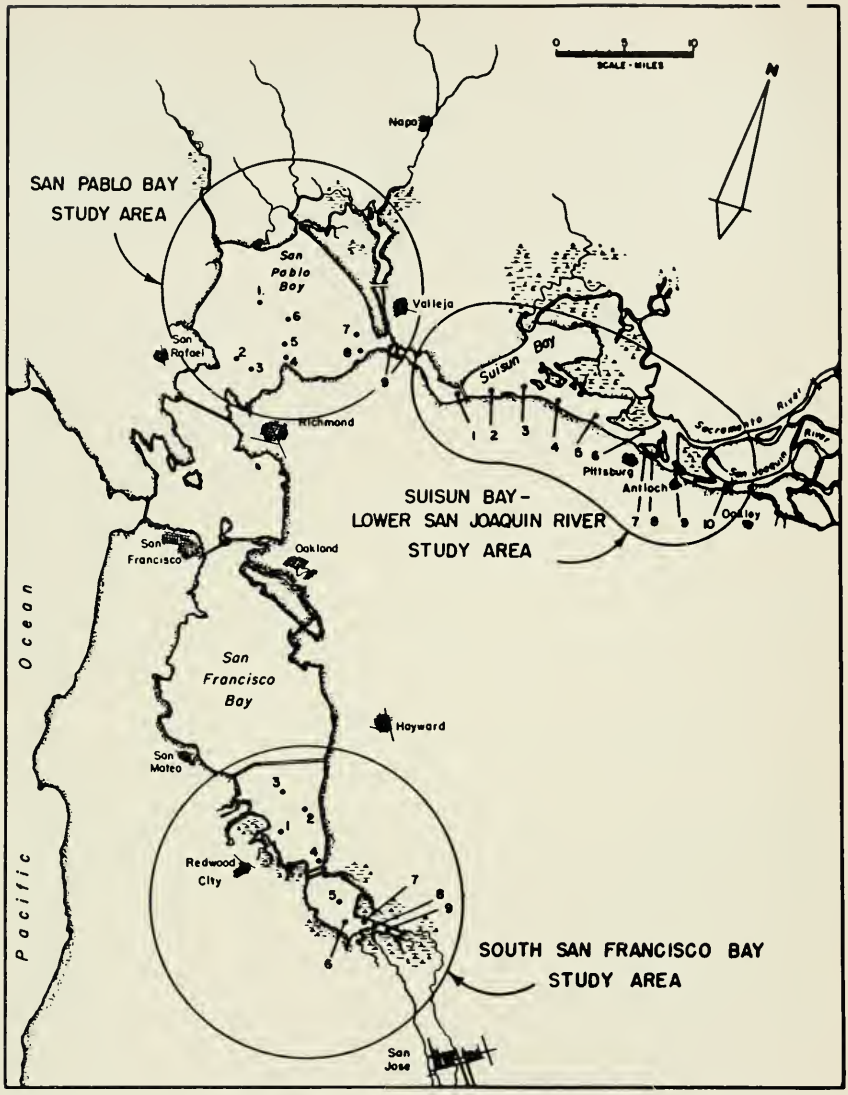

FIGURE 1—Map of San Francisco Bay, showing the areas of study and the locations of sampling stations. (From Storrs, Selleck, and Pearson, 1963.)

Rivers, and is more subject to freshwater influence than the other areas studied. The sampling stations in San Pablo Bay, through which water flows in and out between Suisun Bay and the Golden Gate, are mostly set on either side of the navigable channel, so that stations 2 and 3, 4 and 5, and 7 and 8 might be expected to be rather similar to each other, but stations 1 and 6 are offset from the linear sequence, and should be less affected by dredging and the flow in the channel than the others. The sampling stations in San Pablo Bay do not, therefore, constitute a linear sequence.

METHODS

The samples for this study were taken for the State Water Pollution Control Board. All compilation of data, the water sampling, waste discharge inspection, sediment sampling, and the processing of biological data, other than identification and enumeration of oligochaetes, were made by the University of California for the State Water Pollution Control Board. This material has been presented in reports to the Board (McCarty et al., 1962; Storrs et al., 1963), so only a short description of the methods used in this study up to the time of receipt of the oligochaete specimens is necessary.

The samples, except those from the waste discharges, were collected on a monthly basis during the period July 1961–June 1962. Waste discharges were sampled during the following periods: South San Francisco Bay, February 19–March 1, 1962, April 23–May 3, 1962; Suisun Bay-Lower San Joaquin River, New York Slough, March 11–21, 1962, May 14–24, 1962; San Pablo Bay, April 9–19, June 10–20, 1962; Carquinez Strait, April 9–19, March 11–21, June 10–21, May 14, 1962. Waste discharge samples were taken as near midchannel as possible, so that channel water in particular could be studied, and sediment and benthic samples were taken close to the water sampling sites. Water samples were taken at higher low slack water, higher high slack water, and lower low slack water. In analyzing water samples, the values for higher low and lower low water were averaged together and the resulting figure averaged with the figure for higher high water. This method of averaging gave the clearest impression of average water quality over the four tidal periods (McCarty et al., 1962).

Water samples were taken with a 2- to 3-liter capacity Kemmerer bottle. The basic pattern of sampling was to take three samples at slack water stage: one 2 to 3 feet below the surface; a second 15 feet below the surface; and a third 3 feet above the bottom. The water was analyzed for chemical constituents, generally according to the *Standard Methods for the Examination of Water and Wastewater, 11th Edition.* Cores for studying the sediment constituents were taken with glass tubing with an internal diameter of 30 mm. The benthic fauna was sampled with a 220-cubic-inch orange-peel grab, which was used despite reservations as to its efficacy. Two samples of benthic animals were taken at each station on each sampling date. The material from the grab was washed on the survey boat by a high-volume, low-pressure stream of bay water passing through a 30-mesh screen with 0.5-mm openings. The Sanitary Engineering Research Laboratory of the University of California identified the specimens, but the oligochaetes were not identified to species.

The oligochaetes were counted twice: as a group when they were separated from the other fauna in 1961–1962, and as individual species for this paper. The average number of worms in the reports to the State Water Pollution Control Board is lower than the average count of species made in this study, but the general distribution pattern from station to station is the same for both counts. It is assumed that the difference between the two values is the result of the averaging methods used in the separate counts and small differences in the number of samples available. A number of the oligochaete samples were missing

when the second count was made. For the purpose of this study, the second count is used in comparing the different species, but in instances where oligochaetes as a whole are compared with other fauna or factors, the numbers are taken from the reports to the State Water Pollution Control Board unless otherwise stated. Since samples were missing in the second count, it was impossible to consider seasonal changes. Previous experience with quantitative data on the abundance of oligochaetes also indicates that inaccuracies occur if less than six samples are used to estimate the abundance of oligochaetes at a particular location. Therefore, the average of the data derived from all the samples taken at each station, including those which had a zero figure, is considered as constituting a single set of estimates of the relative abundance of the worms, regardless of the differences in the dates on which the samples were taken.

Since the stations in one of the three areas cannot be regarded as forming an essentially linear series, illustrations could not be in the form of graphs. On the other hand, a graphical style of presentation indicates the sequential changes in two of the areas. Therefore, a compromise system was adopted. In all illustrations, the various value parameters are plotted as symbols but are not connected by lines. Where the same parameter for all three areas appears on a single illustration, different symbols are used to indicate each area. In this manner, values for South San Francisco Bay and Suisun Bay may be read as a sequential series, but those for San Pablo Bay should not be viewed in this way.

WATER AND SEDIMENT QUALITY CHARACTERISTICS

Chlorosity

Maximum chlorosity values (grams per liter chloride ion) for South San Francisco Bay varied little between stations, and the highest values were obtained here. The minimum figures were also relatively high, and the range of values (the difference between the largest and smallest chlorosity values obtained at any one station throughout the study period 1961–62) increased from stations 4 to 9 (Figure 2A, B). A rather similar pattern of values was obtained for San Pablo Bay, but both maximum and minimum values were lower than their equivalents in South San Francisco Bay when the stations are considered in series from seaward to landward. In general, the range of values was greater, indicating a more active mixing of sea water and fresh water.

The chlorosity values in Suisun Bay differed markedly. The most seaward station produced the widest range of values, while the innermost stations received much less salt water than any other area considered in the study.

Saturation with Oxygen

While maximum values for saturation with oxygen fell below 90% at stations 8 and 9 in South San Francisco Bay, and minimum values reached zero from stations 6 to 9, minimum oxygen values were usually well above 60% of saturation in Suisun Bay and San Pablo Bay. Only at stations 1 to 3 did they exceed this value in South San Francisco Bay (Figure 3).

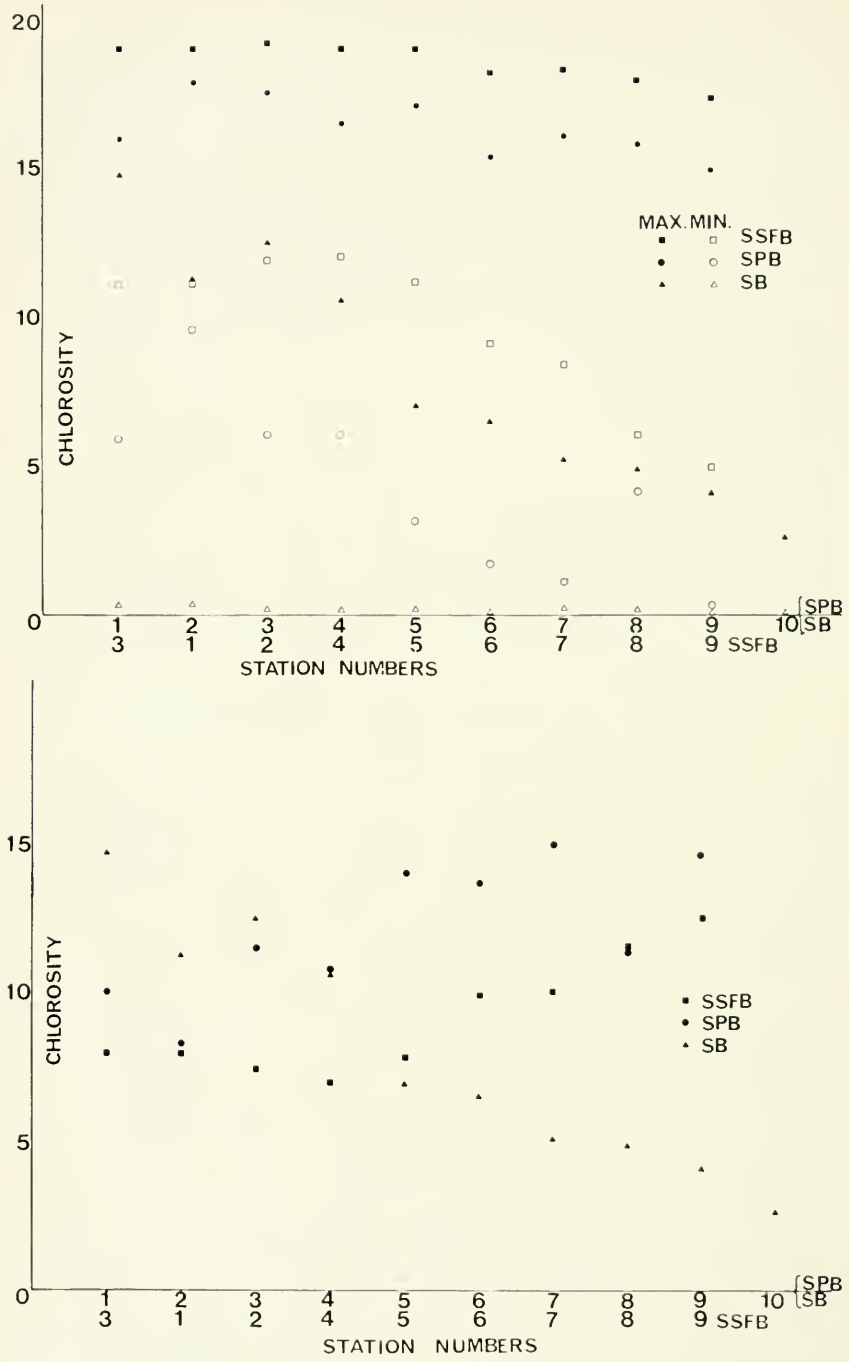

FIGURE 2—A, maximum and minimum chlarosity values (grams per liter chloride) observed at each station; B, range of chlarosity values observed at each station (the difference between the largest and smallest values observed throughout 1961–62).

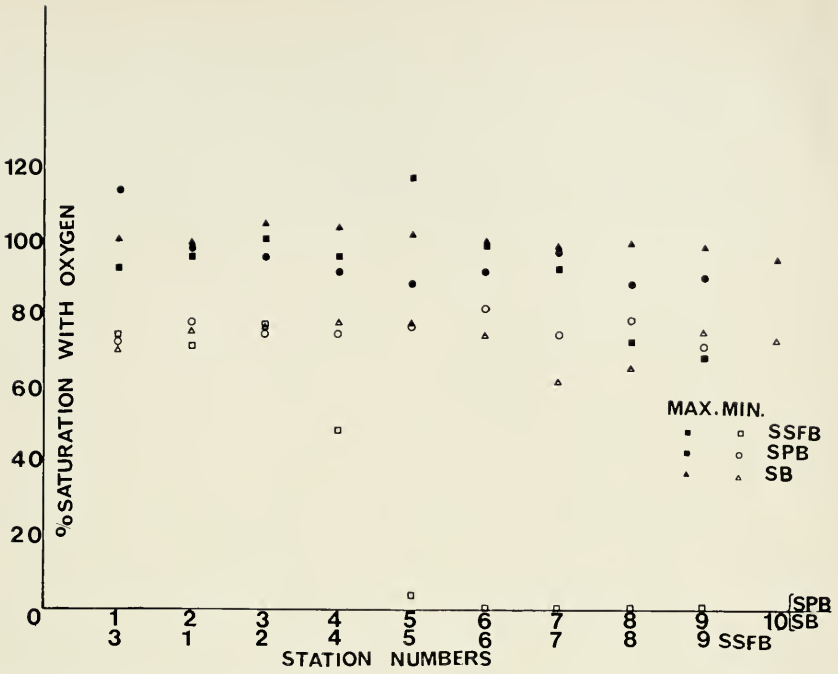

FIGURE 3—Maximum and minimum values for percentage oxygen saturation of water.

Biochemical Oxygen Demand (B.O.D.), Phosphate, and Ammoniacal Nitrogen

Data concerning these dissolved substances show similar trends, with low values at all stations except for the innermost part of South San Francisco Bay. The maximum B.O.D. values in South San Francisco Bay were 2–4 mg/l at stations 2 and 4; 17–22 mg/l at stations 6 and 7; and >200 mg/l at stations 8 and 9; whereas the maximum values at all other sites investigated ranged from 2 to 3 mg/l (with the single exception of San Pablo Bay station 1, where 6.2 mg/l was recorded). Minimum values were usually zero, and were always less than 2 mg/l, except for South San Francisco Bay stations 8 and 9, where values of 2 to 3.7 mg/l were observed.

The full data on these dissolved substances are presented in the published reports for 1961–62 (Storrs et al., 1963).

Temperature

The temperature records show little significant difference between the three bays. Maximum temperatures of 20 to 22 C were usual in Suisun Bay and San Pablo Bay, but were a little higher in South San Francisco Bay (22–27 C). Minimum temperatures lay between 3.5 and 10 C in San Pablo Bay and South San Francisco Bay, but dropped to between 4.6 and 6 C in Suisun Bay. The range in temperatures was least at San Pablo Bay stations 2 to 9 (9.1–11.6 C) and greatest at San Pablo Bay station 1 (20.6 C). At all other stations, temperatures ranged between 12.6 and 18.1 C.

Coliform Bacteria

In order to get an indication of coliform bacterial abundance, the geometric average values given in the 1961–62 reports were summed, and the $\log_{10}$ values considered. The difference between South San Francisco Bay and the other two areas was immediately apparent. The values for South San Francisco Bay stations 1 to 4 were of the same order of magnitude as those for San Pablo Bay and Suisun Bay, but those for stations 5 to 9 reached very high values (Figure 4).

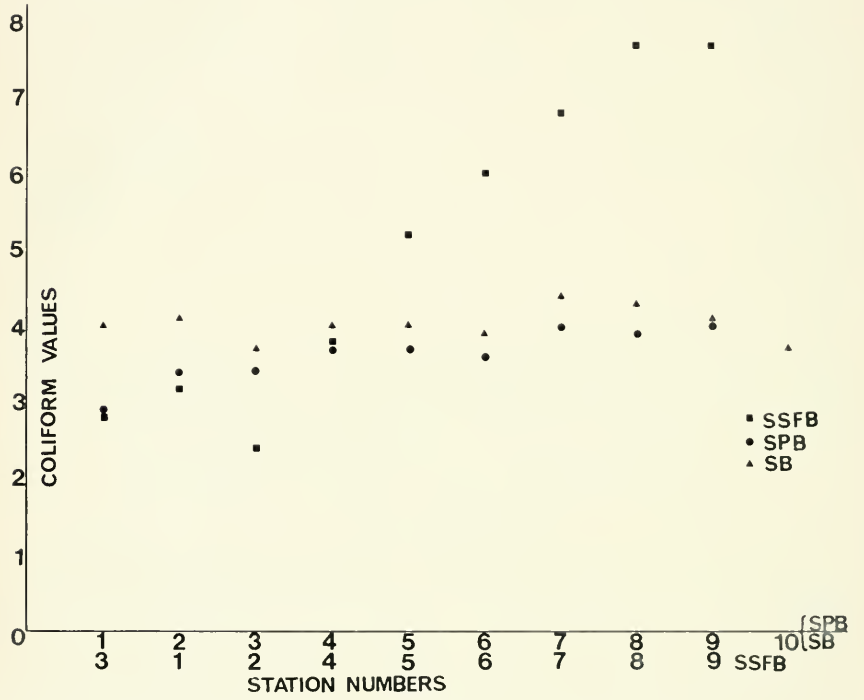

FIGURE 4—Values for coliform bacteria at each station plotted as logarithm of the sum of the average values obtained at each station.

Sediment Characteristics

Various analyses of the sediment samples, including total sulphide, nitrogen, percentage organic carbon, biochemical oxygen demand, and grease (expressed as Hexane Extractable Material or H.E.M.), were made.

Maximum sulphide values were less than 0.5 mg/g at all stations in Suisun Bay, but exceeded this at all other sites except San Pablo Bay station 5. Maximum values exceeded 6 mg/g at San Pablo Bay station 6, and South San Francisco Bay stations 8 and 9. Average values were below 1.5 mg/g at all stations except South San Francisco Bay stations 8 and 9 (3.67 and 4.01 mg/g, respectively).

Biochemical oxygen demand values exceeded 10 mg/g only at South San Francisco Bay stations 8 and 9, Suisun Bay station 4, and San Pablo Bay station 6, but minimum values never exceeded 2.5 mg/g.

Organic carbon values averaged 1 to 2% in San Pablo Bay and South San Francisco Bay, but exceeded these figures at Suisun Bay stations 2, 5, and 8. Maximum values at these three stations reached 36% and values of 13% and 7% were observed at Suisun Bay stations 4 and 10, respectively. At all other stations, maximum values lay below 2.5% (except at San Pablo Bay station 2—4.4%).

Total nitrogen values were high at Suisun Bay stations 2, 5, and 8, where maximum values reached 5.6, 9.7, and 4.8 mg/g, and 3.6 mg/g was observed at Suisun Bay station 4. At all other places, the maximum values never exceeded 2.8 mg/g. Average values were less than 1.7 mg/g except at Suisun Bay stations 2, 5, 7, and 8. The largest average was recorded at Suisun Bay station 7, where the maximum value was only 2.5 mg/g. There is, therefore, quite a good correlation between percentage organic carbon and total nitrogen.

Material provisionally entitled "grease" was extracted by hexane from a stirred water suspension of the sediment. Since the extracted material has not been fully identified, the term Hexane Extractable Material (H.E.M.) is used in preference to grease. It follows that data on H.E.M. should be interpreted with some reservation.

The analyses of H.E.M. are reported as milligrams per kilogram of sediment. The average figures quoted vary from 127 to 1904. The highest values were obtained at Suisun Bay station 5 (1904), San Pablo Bay stations 1 and 6 (802 and 1359, respectively), and South San Francisco Bay station 9 (820). Average values between 500 and 600 were obtained from Suisun Bay stations 7 and 8, San Pablo Bay stations 4 and 7, and South San Francisco Bay stations 1 and 8.

No attempt has been made to correlate the distribution and abundance of worms with particle size. Even though the results of the analyses show considerable variation at any one station, the wide distribution of the few species involved may indicate that the type of sediment found in the study area was suitable for colonization by the worms and that other factors were of greater importance in determining local abundance.

THE OLIGOCHAETA

Species Present

The dominant aquatic oligochaete in the areas studied was *Peloscolex gabriellae* Marcus, a species recorded from several sites in North America, including Point Richmond and Tomales Bay, California (Brinkhurst, 1965). This species was present at every station in the whole area from which worms were received for identification. Two other species, *Peloscolex nerthoides* Brinkhurst and *Peloscolex apectinatus* Brinkhurst, were also widely distributed.

No other oligochaetes were found in South San Francisco Bay. Four specimens of *Paranais frici* Hrabě were found at San Pablo Bay station 9, the station nearest Suisun Bay. This naidid closely resembles *Paranais litoralis* (Müller), which was reported from Point Richmond (Brinkhurst, 1964), and this earlier record therefore should be confirmed.

The fauna of the third area, Suisun Bay, contained three of these saltwater or brackish-water species, *P. frici*, *P. gabriellae*, and *P. nerthoides*, as well as *Limnodrilus hoffmeisteri* Claparéde, a species

normally found in fresh water but known to be tolerant to salt water (Brinkhurst and Kennedy, 1962), and a new form of *Ilyodrilus frantzi* Brinkhurst named *I. frantzi* (*capillatus* form) (Brinkhurst, 1965). The typical form of *I. frantzi* has been found in Lake Tahoe, California/Nevada and in Lake Washington, Seattle.

Species Distribution and Abundance

Since all of the samples containing oligochaetes were not not made available for study, there are differences in the sources of the data used.

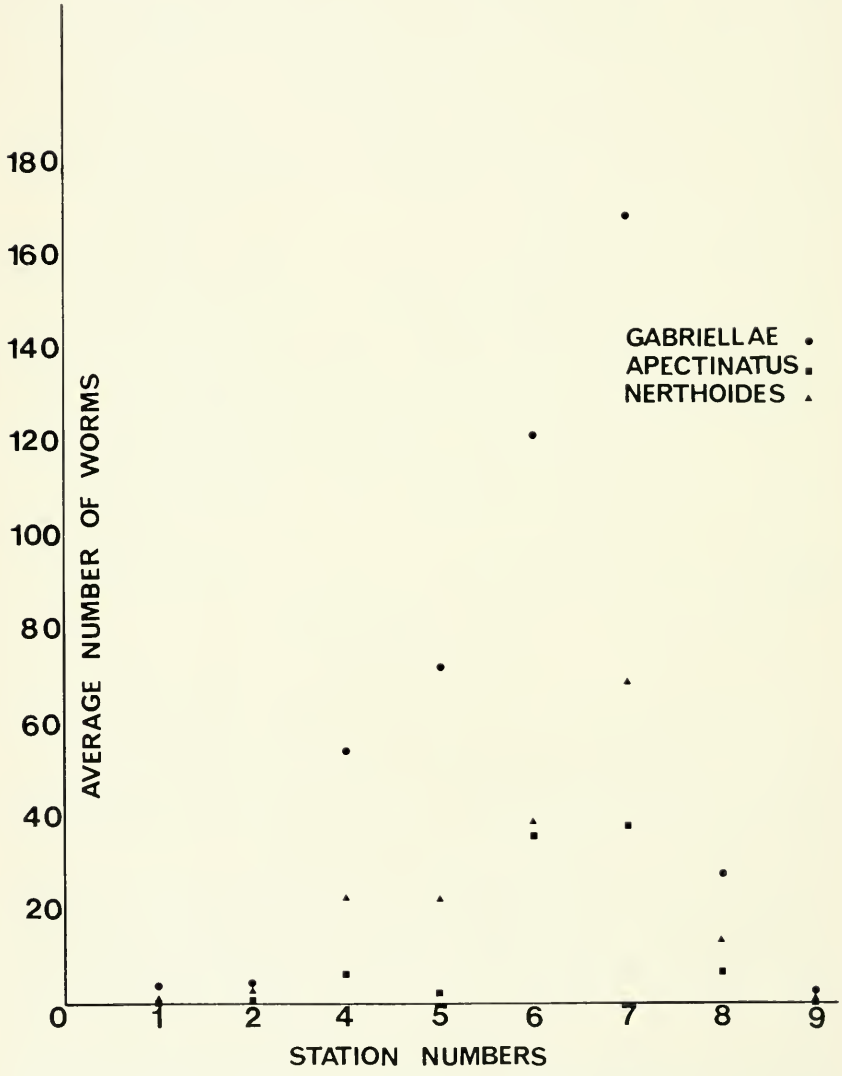

FIGURE 5—The average number of the three species of *Peloscolex* at each station in South San Francisco Bay (no data available for Station 3).

The average number of "animals other than oligochaetes" at each station was derived from the reports (McCarty et al., 1962), as was the percentage of oligochaetes in the fauna at each station. Where the average number of individuals of identified species of oligochaetes is quoted, it was obtained by dividing the total number of specimens examined by the total number of samples taken, including those samples in which no worms were present according to the report. A comparison between the average numbers of oligochaetes cited in the report and the averages for total oligochaetes obtained in the present study indicated that the examination of available samples revealed the same trends as presented in the published report.

The variation in the number of samples examined from any one location makes statistical testing of some of the suggested correlations well-nigh impossible, and makes it necessary to discuss abundance in terms of average numbers per orange-peel grab after washing with a 30-mesh screen.

South San Francisco Bay [3]

In South San Francisco Bay all three species of *Peloscolex* were found at each station. All three became increasingly abundant at stations 1 through 7, but there was a dramatic reduction in the abundance of worms at station 8, and at station 9 the worms were as scarce as at stations 1 and 2 (Figure 5). The number of animals other than oligochaetes varied in the same way (Figure 6).

[3] No samples were received from station 3.

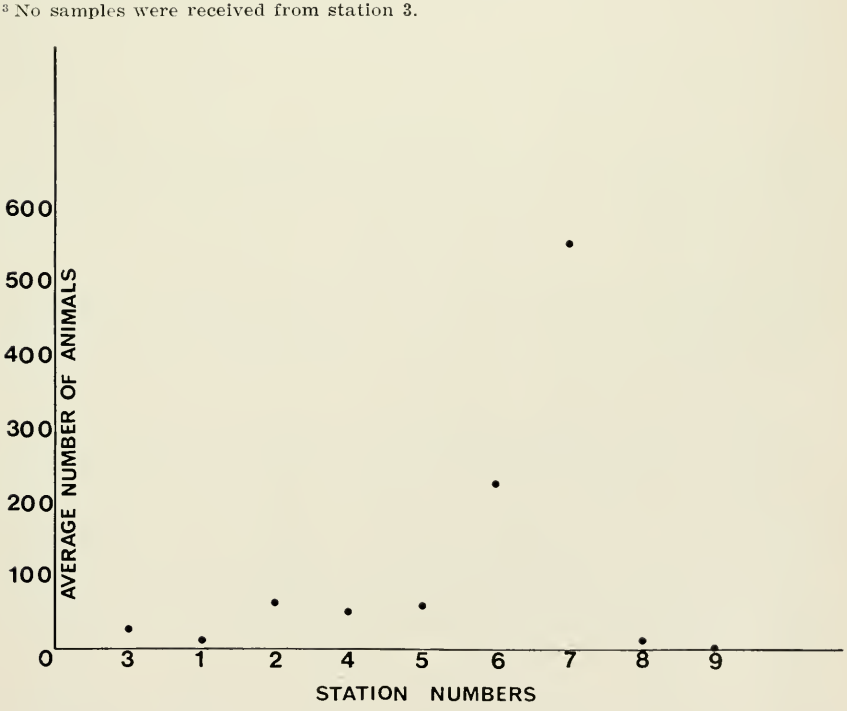

FIGURE 6—The average number of "animals other than oligochaetes" at each South San Francisco Bay station.

The number of identified taxa varied from 2.6 to 14.2 (average 10.9) at all stations except 8 and 9 (average 3.6 and 2.3, respectively) and the percentage of oligochaetes in the fauna showed an upward trend from station 3 through station 9 (Figure 7).

FIGURE 7—The percentage of oligochaetes in the bottom fauna at each South San Francisco Bay station.

San Pablo Bay

In San Pablo Bay, *P. gabriellae* was the only abundant species, the average values for the other oligochaetes being less than one per station.

The average number of *P. gabriellae* per sample was highest at station 9, where the range of chlorosity and the coliform bacteria count was the highest for the bay (Figure 8). The values for these parameters at stations 7 and 8 were somewhat lower than at 9, and the average number of worms was about half that observed at the latter station. The numbers of worms were lower again on the shoreward side of the channel (stations 3 and 4), still lower to the north of the channel (stations 1, 5, and 6), and reached a minimum at station 2. The percentage of worms in the fauna was variable, but was highest on the south side of the channel (stations 3, 4, and 8) and at station 7. The mean total number of all animals in the bay was fairly constant, but there was a dramatic increase at station 9.

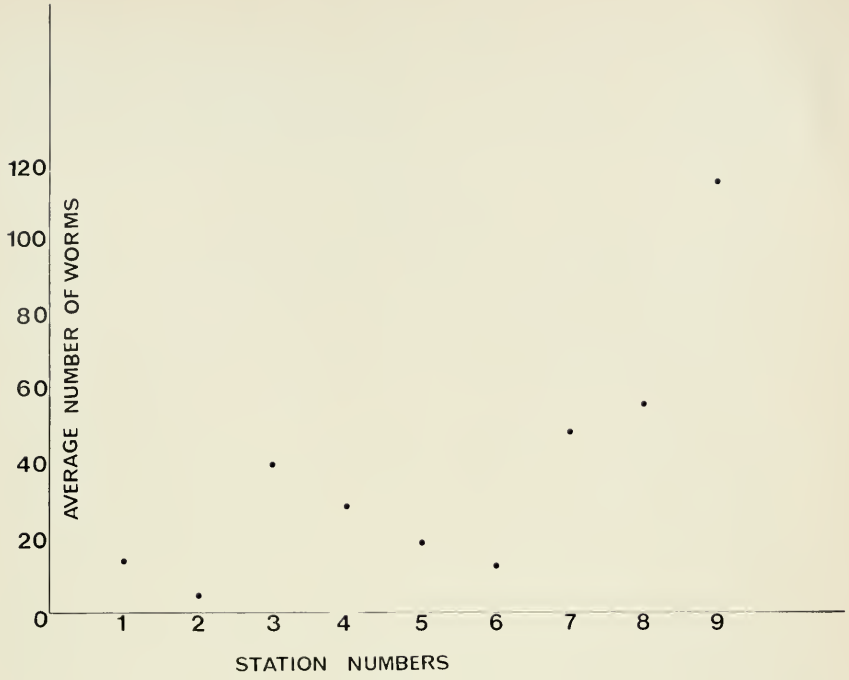

FIGURE 8—The average number of *Peloscolex gabriellae* at each San Pablo Bay station.

Suisun Bay

Worms were very scarce at stations 1 to 5, and no samples were available for study. At stations 6 to 10 the numbers of worms were of the same order of magnitude as in San Pablo Bay (except station 9), but *P. gabriellae* was scarce here. The most abundant species was *L. hoffmeisteri*, a predominantly freshwater form, and the naidid *P. frici*, which has been reported from fresh and brackish water (Table 1). The average number of *L. hoffmeisteri* was fairly constant, but fell off markedly at station 10. It reached a maximum value at station 7, where *P. frici* was also most abundant.

TABLE 1

The Distribution and Abundance of Oligochaete Species in Suisun Bay, and Percentage of Oligochaetes in the Bottom Fauna

Station	*Limnodrilus hoffmeisteri*	*Peloscolex gabriellae*	*Peloscolex nerthoides*	*Ilyodrilus frantzi capillatus*	*Paranais frici*	*Oligochaete percentage in bottom fauna*
1–5	---	---	---	---	---	0–0.1
6	30.6	2.1	0	0.1	1.7	65.6
7	47.5	0.5	0	0	6.7	91.2
8	36.7	0.5	0	0.2	0.1	97.8
9	36.5	0.1	0	2.6	1.4	73.5
10	8.0	2.3	0.3	0	0.3	9.7

Oligochaetes made up more than 90% of the bottom fauna at stations 7 and 8, more than 50% at stations 6 and 9, but less than 10% at all other points. The average number of individuals was low at all stations, the maximum value being lower than the lowest number of entities recorded at any station in the other two bays except for the most grossly polluted part of South San Francisco Bay (station 9).

DISCUSSION

A comparison between worm distribution and abundance and the sediment and water quality data suggests that the very marked pollution at South San Francisco Bay stations 8 and 9 not only is correlated with the reduction of both the number of animals (including oligochaetes) and the number of types of animals present, but also with a rise in the proportion of oligochaetes in the fauna. Conditions at South San Francisco Bay stations 6 and 7 may be considered as creating an area of enrichment. The sediment and water quality is markedly better than at stations 8 and 9 (although zero oxygen values have been reported), and the organic material is now indirectly available as food for a large, more diverse population of animals. This observation is supported by comparison with other areas. The average number of animals nowhere exceeded 100 except at San Pablo Bay station 9, where the average value of 427 was still less than half that for South San Francisco Bay station 7. Coliform bacteria counts were higher at South San Francisco Bay stations 6 to 9 than at any other site, which reflects the quantity of available organic matter.

The decrease in the abundance of organisms from stations 7 to 2 should not be regarded as unusual, particularly since the diversity of the population reaches a maximum at South San Francisco Bay station 2 (14.2). The drastic reduction in diversity and total numbers of organisms at station 1, and station 3 to a lesser extent, may well reflect local pollution of a different type. The sediment and water quality tests do not reveal any evidence of gross organic pollution at station 1, but the H.E.M. value was high. The H.E.M. values were also high at stations 8 and 9, so that the paucity of organisms at these stations may be due to more than excess organic pollution. Analyses of waste discharges in the area adjacent to stations 1 and 3 indicate that a considerable amount of heavy metal waste flows into the bay via Redwood Creek (Storrs et al., 1963), which may be responsible for the reduction in the fauna, especially the oligochaetes.

Most of the waste discharges reaching San Pablo Bay enter via the Napa River, the shores around Carquinez Bridge (close to station 9), or along the south shore of the channel close to San Pablo Bay station 8 and, to a lesser extent, stations 3 and 4. Many of these are sewage outfalls, so that the number of worms at these stations may well be correlated with the amount of organic matter available as a substrate for bacteria and/or fungi. Similarly, the high mean total number of all animals noted at San Pablo Bay station 9 may be related to the coexistence of a rich food supply and the water current flowing to and from Suisun Bay.

In a detailed study of the effects of the Castro Creek effluents reaching San Pablo Bay, Filice (1954) suggested that the restricted faunal

diversity combined with a rich food supply helped to maintain very large animal populations on the south side of the navigable channel. The scouring in the channel produced a predominantly sandy substrate which supported few animals, and the area immediately in the path of the waste water flowing from the creek was uninhabitable because of a shortage of oxygen and the presence of unabsorbed toxic materials.

The difference in the worm species present in Suisun Bay probably reflects its more "estuarine"[4] nature, as evidence by the chlorosity values. In view of the low average number of entities recorded, the changes in the percentage representation of oligochaetes in this bay must be interpreted with caution. However, the consistent way in which these changes occur between stations 5 and 10 suggests that this may not be a chance phenomenon. While optimum salinity gradients may explain the abundance of *P. frici* at Suisun Bay station 7, the same argument can scarcely be advanced to account for the abundance of *L. hoffmeisteri* at that point.

The poor bottom fauna found at Suisun Bay stations 1–5 is also difficult to explain except that few species are specially adapted to occupy the strictly brackish-water localities which lie beyond the penetration range of the most tolerant marine or freshwater species. It would be difficult to attribute the scarcity of fauna in this region to the effects of pollution, as one would expect such drastic pollution loads to affect San Pablo station 9, especially since many additional effluents enter the system in the region of that station. Instead, the average number of oligochaetes as well as of other animals is high at San Pablo Bay station 9, where the diversity is also much greater than at Suisun Bay station 1, despite the fact that the two are separated only by Carquinez Strait. Filice (1958) reported a marked reduction in the faunal diversity between Carquinez Strait and Point Suisun as compared with a slight change in faunal diversity between Point San Pablo and Carquinez Strait and between Point Suisun and the Antioch Bridge. Day (1951) reported that euryhaline marine species may penetrate an estuary to the point where the average salinity reaches 5‰, although few are able to penetrate water with a salinity of less than 15‰. The average salinity values for the seaward and landward ends of Carquinez Strait were reported as 15‰ and 10‰, respectively, by Filice (1958), who stated that the major faunal change takes place in Carquinez Strait. It is noticeable that *L. hoffmeisteri* was found farther out in the estuary than the single previous record (Filice, 1958) would suggest.

The aquatic oligochaetes are of value in pollution detection surveys in rivers and lakes, especially if the number of worm species, their relative abundance, and their abundance in relation to the diversity and abundance of the rest of the bottom fauna are recorded (Brinkhurst, 1966*a*,*b*). There are few brackish-water and marine species of oligochaetes, and hence they are of limited value in attempts to detect pollution in saline water, as the reduction in diversity cannot be very great. Even here significant changes in abundance of certain species may yield good supporting evidence of the nature and source of pollution materials.

[4] This term is used to mean a region subject to wide fluctuations in chlorosity as opposed to a brackish-water region of more constant chlorosity.

SUMMARY

San Francisco Bay may be divided into three major zones with respect to oligochaete distribution in relation to salinity. The least saline area, the innermost part of Suisun Bay, contains predominantly freshwater species as well as brackish-water forms. The most estuarine part, the outermost part of the Suisun Bay area to Carquinez Strait, contains few benthic invertebrate animals of any sort. The majority of the area studied is predominantly brackish water, and the tubificid *Peloscolex gabriellae* occurs in abundance.

The effect of organic pollution is to reduce the diversity of the fauna. Under grossly polluted conditions, oligochaetes make up a high proportion of the fauna but are few in number. In zones where the supply of nutrients from sewage is great, but toxic wastes are absent or have been absorbed and the oxygen levels are good, worms occur in extremely high numbers.

ACKNOWLEDGMENTS

This work was carried out with the help of a research grant from the U.S. Public Health Service, WP-00521. We are indebted to R. A. Wagner for the gift of the material, which was analysed while the authors were at the University of Liverpool, England. We are also indebted to P. N. Storrs, Project Engineer, Richmond Field Station, for providing copies of the reports and for permission to publish the results.

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JACK MACKEREL YIELD PER AREA FROM CALIFORNIA WATERS, 1955–56 THROUGH 1963–64[1]

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Marine Resources Operations
California Department of Fish and Game

The commercial catch of jack mackerel, *Trachurus symmetricus*, ranged from 11,352 to 54,707 tons per season during the period 1955–56 through 1963–64. Southern California waters were the most productive, accounting for 90% of the total catch in all but three seasons. During the first three seasons, catches totaled 97,764 tons, with 72% taken from inshore areas off southern California. The next three-season group produced only 69,968 tons. Less than 38% of this was from southern California inshore waters, while the offshore waters contributed 45%. The last three seasons produced 145,167 tons, with 62% taken in the offshore regions of southern California. This shift in catch localities seems to be caused partly by a decline in the sardine fishery. Other possible factors have not been analyzed to date.

INTRODUCTION

Yield-per-area reports are useful when studying the relationship of a fish to its environment or in analyzing major changes in population location that may have affected the success of a fishery.

This is the second article dealing with jack mackerel yield per area from California waters. The first article covered the period 1946–47 through 1954–55 (Clothier and Greenhood, 1956). The present article covers the 1955–56 through 1963–64 seasons. Each group of three consecutive seasons had similar areas of catch distributions. The data for the similar seasons are combined and presented pictorially (Figures 1, 2, and 3).

Roedel (1953) discusses the basis for using other than a calendar year for the fishing season. Based historically upon the sardine, *Sardinops caeruleus*, and Pacific mackerel, *Scomber japonicus*, fisheries, the season is considered as opening in May and extending through the following April. Therefore, the landings in this report are presented on the same seasonal basis.

The data for this report were prepared and tabulated by the Biostatistical Unit Marine Resources Operations from source data resulting from the California "pink ticket" system (California Bureau of Marine Fisheries, 1952). The source data consist of fish receipts filled in by the dealer at the time the fish are unloaded. These receipts list the kinds of fish taken, pounds landed, and the block area of catch.

Sometimes the dealers do not enter the catch areas on the fish receipts and to insure that the best information pertaining to each catch is included in our statistical system, two other data sources are utilized. During the sardine season the Department employs "checkers" who make out a special checker's ticket for each boat delivering fish to a

[1] Submitted for publication October 1967.

cannery. The ticket includes block area of catch, species composition, and other information pertaining to the landing. Scientific personnel also request block area information from the vessel captain when taking routine samples of his catch. With these sources of information, the block area of catch remains unknown for only a small portion of the landings; approximately 6% each year (Table 1).

CATCH AREAS

The primary fishing grounds for jack mackerel are located off southern California from Point Conception to San Diego and offshore as far as San Nicolas Island and Tanner and Cortes Banks. The catch from this area generally accounts for 80 to 90% of the statewide total. The other 10 to 20% of the catch is taken off central California, from Monterey Bay to Point Conception.

The block origins off southern California have been grouped into 11 general areas which represent natural fishing grounds (Table 1). These general areas may be combined into three regions. The close inshore region is composed of the general areas of Santa Barbara, Port Hueneme, Point Vicente, Oceanside, and San Diego. The offshore region is composed of the northern Channel Islands area, the Santa Barbara Island area, and the Santa Catalina Island area. The distant offshore region consists of the San Nicolas Island, San Clemente Island, and Tanner and Cortes Banks areas.

During the period 1955–56 through 1957–58, the close inshore region produced 72% of the total statewide catch, the offshore region 11%, and the distant offshore region 9% (Figure 1). In the next three-season period, 1958–59 to 1960–61, the area of catch shifted offshore somewhat, with the offshore region accounting for 42% of the total catch and the distant offshore region 3%, while the close inshore region produced less than 38% (Figure 2).

The shift in the area of catch was even more apparent during the 1961–62 through 1963–64 seasons, when the distant offshore region supplied 34% and the offshore region 28% of the catch, while the close inshore region produced only 29% (Figure 3).

DISCUSSION

Clothier and Greenhood (1956) discussed the difficulty of analysis of the jack mackerel fishery, because of its relationship to the sardine and Pacific mackerel fisheries.

The same fleet of vessels fishes for both sardines and jack mackerel. During the sardine season, the fleet is searching primarily for sardines, but will take mackerel if sardines are not available on the fishing grounds. Consequently, the catch areas of mackerel tend to reflect the search for sardines[2]. Clark (1937), in an analysis of sardine catch areas, concluded that most fish are taken within 3 to 5 miles of shore (including islands) and in waters less than 500 fathoms deep.

There were, however, some periods when sardines were very scarce. For the periods corresponding to the three-season groups in this article, the approximate sardine catch was: 1955–56 through 1957–58,

[2] This is applicable only to the period covered in this report. Since 1964 sardine landings have continued to decline, resulting finally in a 2-year moratorium on sardine fishing, effective June 7, 1967.

TABLE 1

Jack Mackerel Catch by General Fishing Areas, May Through April

General area	Block numbers	1955–56		1956–57		1957–58		1958–59		1959–60		1960–61		1961–62		1962–63		1963–64	
		Tons	%	Tons	%	Tons	%	Tons	%	Tons	%	Tons	%	Tons	%	Tons	%	Tons	%
Pt. Arena	401–421	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--
Bodega Head	422–445	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
San Francisco	446–471	--	--	2	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--
Pigeon Pt.	472–506	--	--	2	--	--	--	1	--	--	--	1	--	--	--	1	--	--	--
Monterey	507–531	26	.1	621	1.4	931	5.0	1,592	16.6	1,926	6.0	757	3.1	1,575	3.1	794	1.7	824	2.1
Pt. Sur	532–552	--	--	4	--	1	--	1	--	2,217	7.0	27	.1	110	.2	117	.3	--	--
Piedras Blancas	553–606	1	--	--	--	--	--	10	--	134	.4	4	--	178	.3	--	--	148	.4
Pt. Buchon	607–630	--	--	--	--	977	5.2	325	3.4	9	--	--	--	--	--	167	.4	61	.2
Pt. Sal	631–648	--	--	--	--	--	--	--	--	3	--	11	--	--	--	--	--	34	.1
Santa Barbara	651–657, 665–671	195	.7	382	.8	403	2.2	127	1.3	302	.9	548	2.3	979	2.0	246	.6	1,267	3.2
Port Huenemе	664, 680–683, 703–706, 722–725	6,133	21.7	10,225	22.3	7,317	39.4	4,488	46.8	8,367	26.2	2,158	9.0	2,599	5.1	3,372	7.4	2,140	5.5
Northern Channel Islands	684–690, 707–713, 726–732	672	2.4	2,929	6.4	3,749	20.2	1,649	17.2	7,404	23.3	11,253	46.9	13,635	26.6	4,918	10.8	3,681	9.4
Pt. Vicente	679, 701, 702, 718–721, 737–742	9,122	32.3	20,773	45.4	3,007	16.2	687	7.2	5,698	17.9	3,563	14.9	5,671	11.1	7,785	17.1	12,609	32.2
Oceanside	756–758, 801–804, 821–825	4,378	15.5	4,576	10.0	456	2.4	102	1.1	56	.2	154	.7	704	1.4	1,579	3.5	862	2.2
Santa Catalina Island	759–762, 805–808	1,160	4.1	1 557	3.4	486	2.6	128	1.3	4,479	14.1	3,172	13.2	3,964	7.7	2,590	5.7	9,197	23.5
Santa Barbara Island	743–745, 763–765, 809–811	92	.3	146	.3	66	.4	--	--	1,184	3.7	131	.5	528	1.0	246	.5	1,247	3.2
San Nicolas Island	746–749, 766–769, 812–815, 833–836	40	.2	--	--	--	--	--	--	61	.2	358	1.5	4,455	8.7	2,657	5.8	222	.5
San Diego	842–846, 860–864, 877–882	2,624	9.3	460	1.0	44	.2	--	--	8	--	228	1.0	558	1.1	407	.9	1,489	3.8
San Clemente Island	826–832, 847–853, 865–869	3,704	13.1	4,130	9.0	884	4.8	485	5.1	33	.1	1,629	6.8	9,701	19.0	10,638	23.4	3.239	8.3
Tanner and Cortes Banks	854, 855, 870–873, 885, 888–891, 897	80	.3	--	--	267	1.4	--	--	--	--	11	--	6,518	12.7	9,960	21.9	2,128	5.4
Totals		28,227	100.0	45,807	100.0	18,590	100.0	9,595	100.0	31,881	100.0	24,005	100.0	51,175	100.0	45,477	100.0	39,148	100.0
Tons of unknown origin not included above		1,447		2,366		1,327		1,757		1,449		1,281		3,532		2,945		2,890	
Total season's catch		29,674		48,173		19,917		11,352		33,330		25.286		54,707		48,422		42,038	

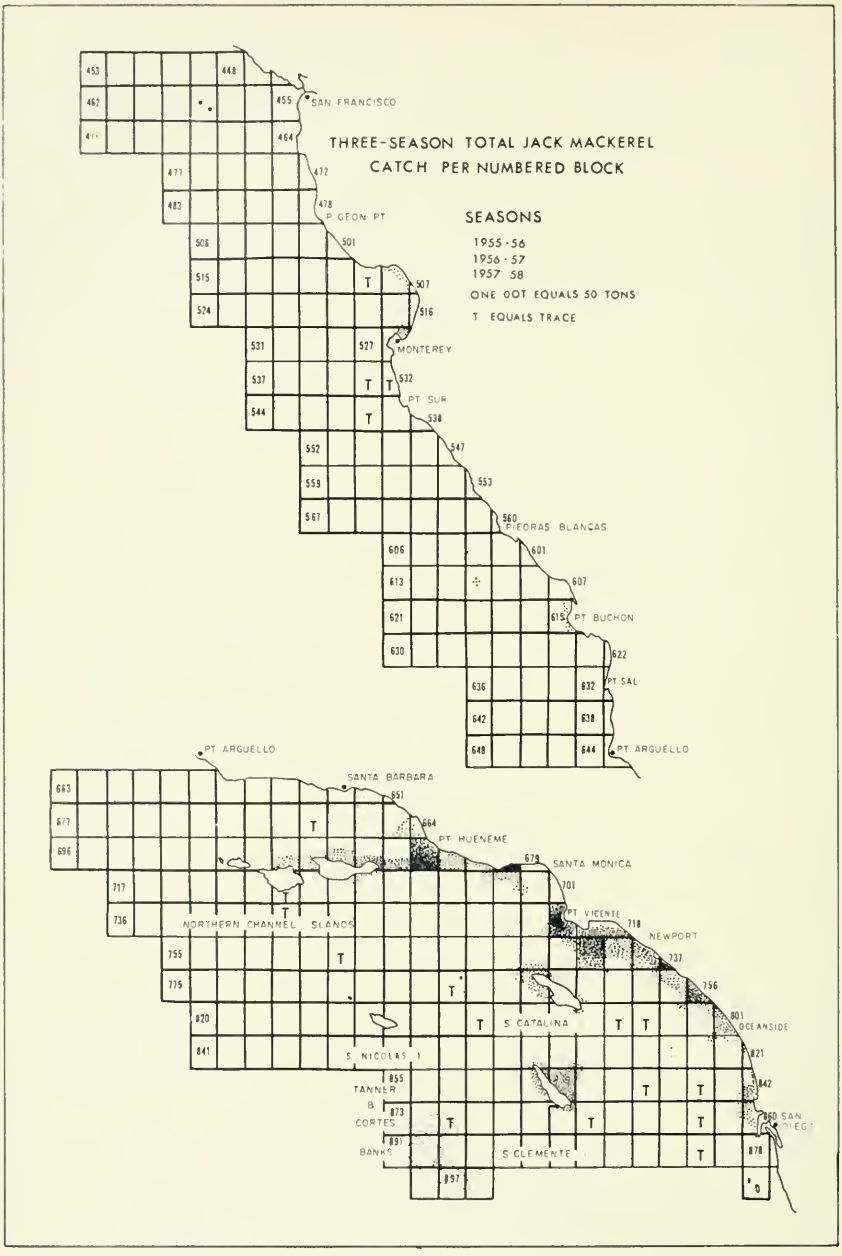

FIGURE 1—Three-season total jack mackerel catch per numbered block; seasons 1955–56, 1956–57, and 1957–58.

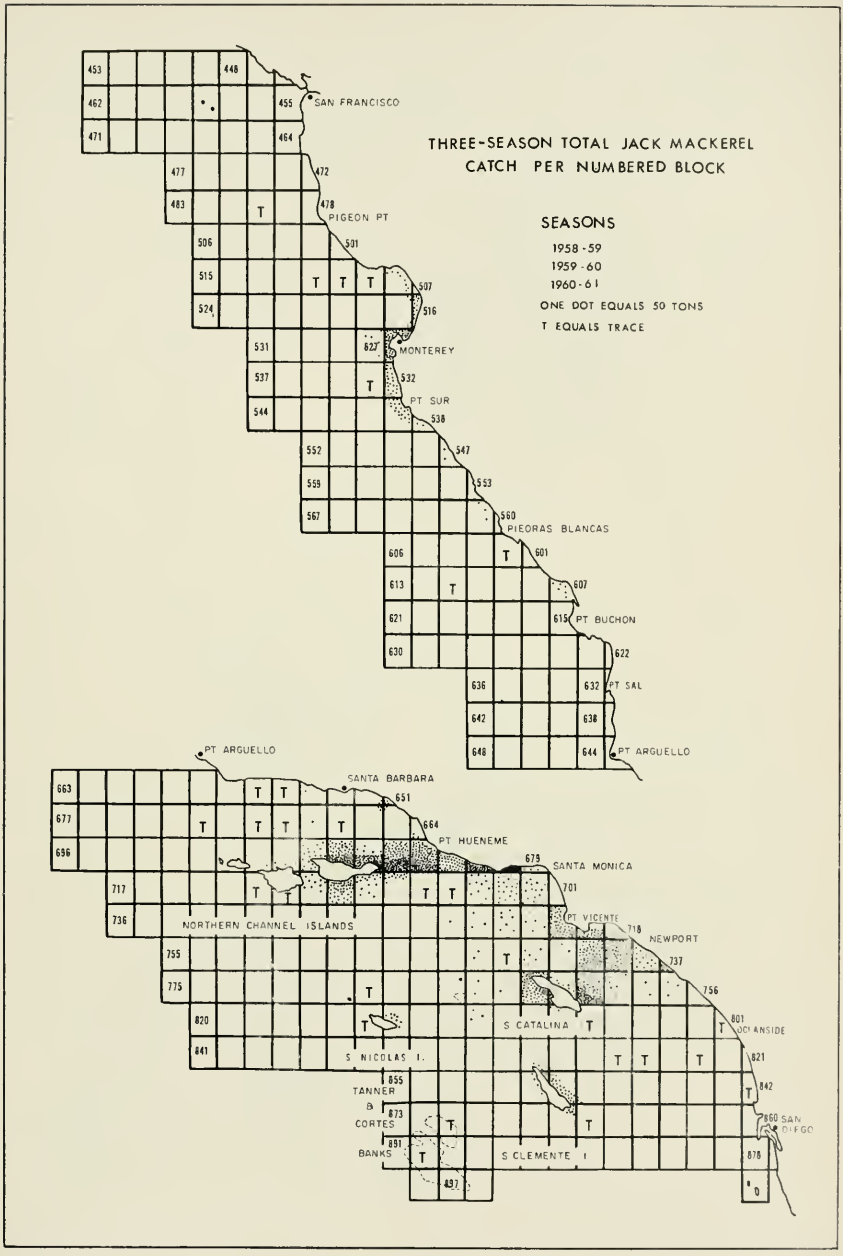

FIGURE 2—Three-season total jack mackerel catch per numbered block; seasons 1958–59, 1959–60, and 1960–61.

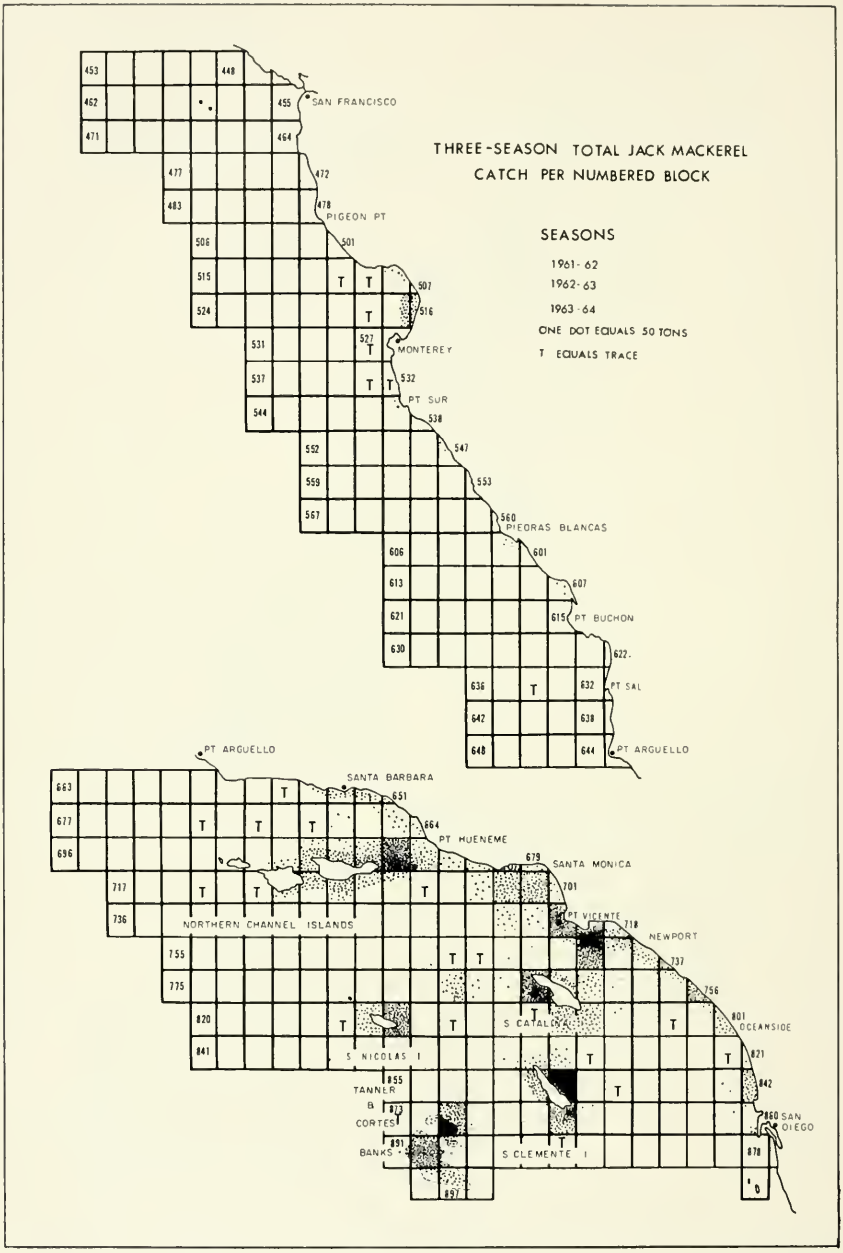

FIGURE 3—Three-season total jack mackerel cotch per numbered block; seasons 1961–62, 1962–63, and 1963–64.

130,000 tons; 1958–59 through 1960–61, 170,000 tons; and 1961–62 through 1963–64, 32,500 tons (Figure 4). The 1961–62 through 1963–64 period produced less than $\frac{1}{5}$ the poundage of sardines taken during the previous three-season period. At the same time, jack mackerel catches for the 1961–62 through 1963–64 seasons were more than double those of the 1958–59 through 1960–61 seasons.

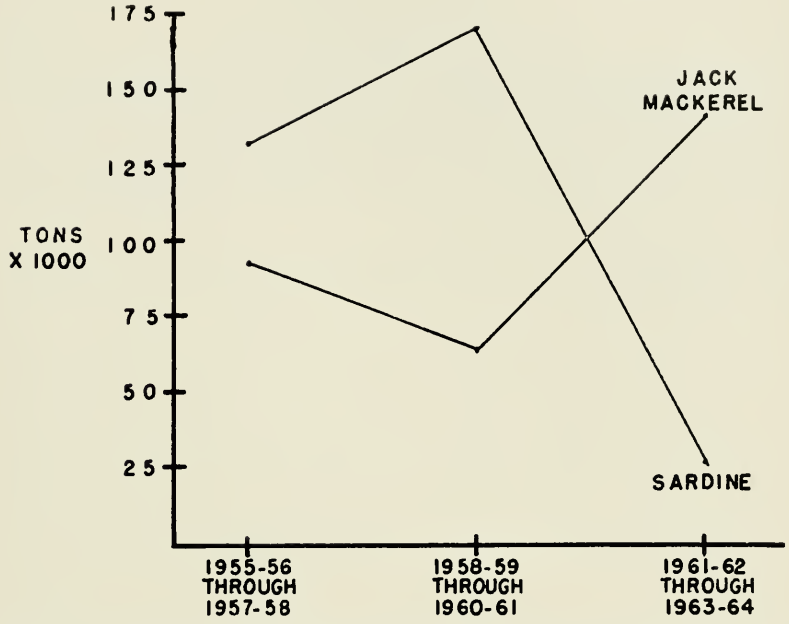

FIGURE 4—Comparative sardine-jack mackerel catches, to the nearest thousand tons, for three three-seasan groups, 1955–56 through 1963–64.

During the 1961–62 through 1963–64 seasons, fishing effort was more specifically pointed at jack mackerel, and the catch areas for this period tend to reflect the actual distribution of jack mackerel. As mentioned previously, there has been an offshore shift in jack mackerel catches during the nine seasons covered in this article, with the heaviest offshore catches being made in the 1961–62 through 1963–64 seasons.

Clothier and Greenhood reported a parallel case for the 1952–53 through 1954–55 period, when a decline in sardine catches resulted in increased offshore jack mackerel catches. These two periods suggest that the center of abundance of jack mackerel tends to be far offshore.

Other factors affecting the apparent abundance of jack mackerel on the fishing grounds include availability to the fishermen, and changes in actual abundance within these fishing areas. We are currently processing 20 years of back data on jack mackerel commercial landings. These data include information on the year-class composition of the landings over this period. From an analysis of the year-class data, some inferences may be made as to changes in actual abundance.

CONCLUSIONS

During the nine seasons covered in this report, there has been an offshore shift in jack mackerel catches in southern California. This seems to be caused by increased scouting for jack mackerel as the sardine fishery continued to decrease, and suggests that the center of abundance of jack mackerel tends to be far offshore.

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INTESTINAL GROWTHS IN THE EUROPEAN FLAT OYSTER, *OSTREA EDULIS*[1]

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Intestinal growths were noted in a European flat oyster during a routine histological examination. These growths were composed of relatively normal epithelial cells and were covered with normal-appearing cilia. A moderate leucocytic infiltration was noted in each growth. It is suggested that these growths may be the end portions of a long ridgelike growth.

INTRODUCTION

Although abnormal growths in mollusks are comparatively rare, several have been recorded in the literature. Tumors in gastropods have been noted by Szabó and Szabó (1934), Gersch (1950), and Fischer (1954). Tumors and tumorlike growths in freshwater mussels, *Anodonta* sp., have been observed by Williams (1890), Collinge (1891), Butros (1948), and Pauley (1967). Ryder (1887) and Smith (1934) each described a mesenchymal tumor in the Eastern oyster, *Crassostrea virginica*, and Sparks et al. (1964*a*) described a similar tumor from the giant Pacific oyster, *Crassostrea gigas*. Sparks et al. (1964*b*) described a tumorlike fecal impaction in the rectum of *C. gigas*. Hueper (1963) observed papillary tumors around the rectum of soft-shell clams, *Mya arenaria*.

During a routine histological examination of oyster tissue, intestinal growths were observed in a European flat oyster. Because of the scarcity of information concerning such growths in mollusks, it seems appropriate to describe these abnormalities.

METHODS AND MATERIALS

The oyster with the intestinal abnormalities was collected from an experimental population in Drakes Estero, near San Francisco, California. A 5-mm cross section was removed from its palp region, fixed in Davidson's solution, dehydrated, embedded, sectioned (at 7 microns), and stained with Harris haematoxylin and eosin using standard methods.

HISTOPATHOLOGY AND DISCUSSION

The intestine of an oyster runs anteriorly from the style sac and passes over the dorsal side of the animal, proceeding posteriorly to the anus. A cross section of an oyster taken from the palp region contains

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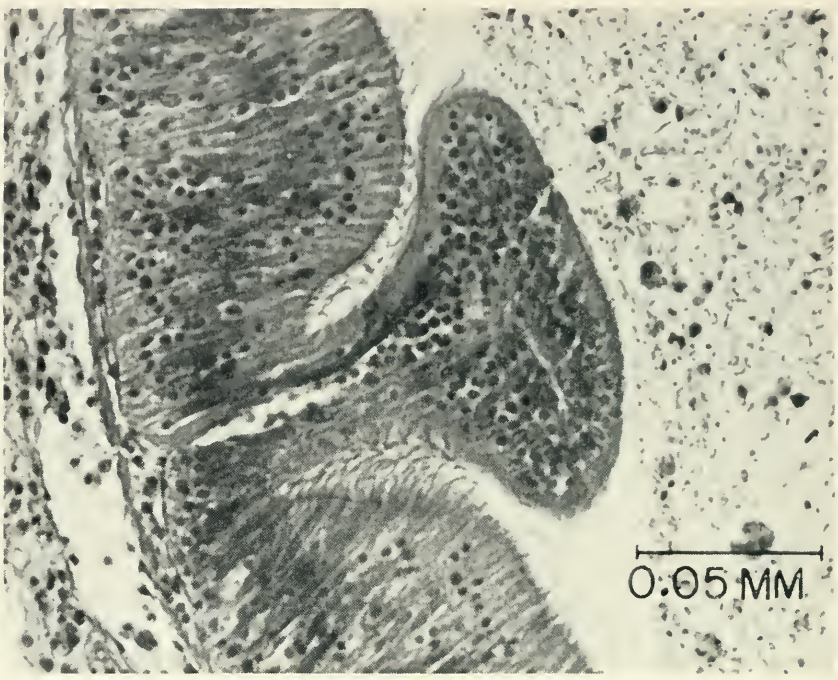

FIGURE 1—The anterior growth in the intestine of *Ostrea edulis*.

two sections of the intestine, one more anterior than the other. Both of the intestinal cross sections prepared from this oyster bore anomalies.

The anterior anomalous growth arises from a slight depression in the intestine opposite the typhlosole (Figure 1). It is mushroom-shaped, measuring 0.15 mm in height and 0.12 mm in greatest width, with the stalk 0.04 mm in width. Microscopically, the growth consists of slightly modified epithelial cells. Relatively normal epithelial nuclei are seen in the stalk of the growth. Nuclei above the stalk indicate that the epithelial cells there are folded over because these nuclei seem to be cut in cross section rather than the expected longitudinal section. A moderate leucocytic infiltration of the growth is evident. Relatively normal cilia are present over the growth, although they appear much shorter on the larger portion of the growth. A vacuolation is especially evident in the stalk of the growth. Close observation reveals that this vacuolation may have resulted from the separation of adjacent epithelial cells. There is a pore in the basement membrane underlying the intestinal epithelium, through which four leucocytes appear to be in the process of entry (Figure 2).

The posterior anomalous growth occurs in the same relative position and is similar to the anterior growth. This growth lacks the well-defined stalk and measures 0.15 mm in height and 0.20 mm in greatest width (Figure 3). It also is composed of modified epithelial cells and is covered by normal cilia. A heavier leucocytic infiltration is more evident than in the anterior growth.

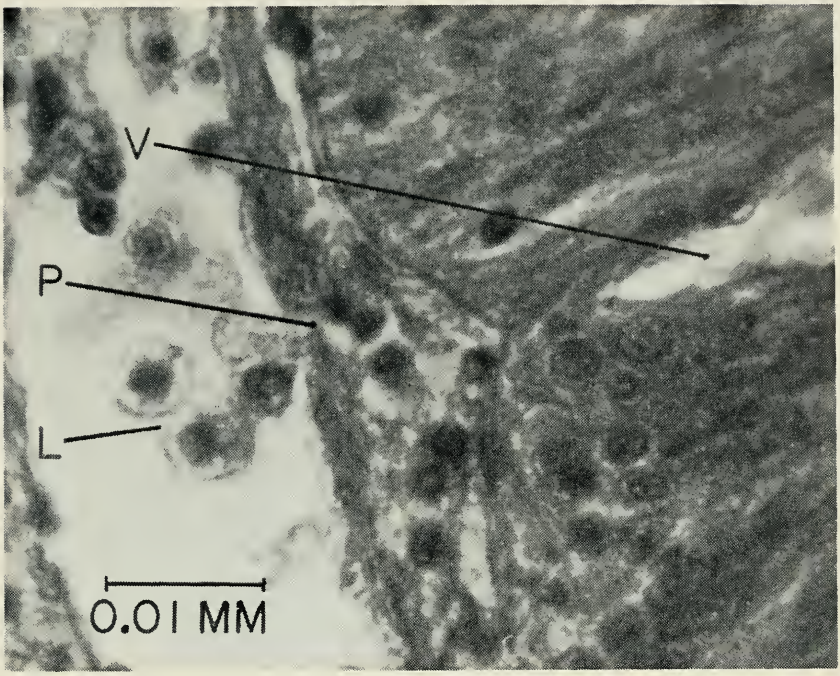

FIGURE 2—The base of the anterior growth, showing the pore in the basement membrane and leucocytes in the process of entry. V = vacuolation, P = pore, L = leucocyte.

The origin of these growths and their effects on the oyster are unknown. Such anomalies are not visible externally; therefore, their detection and subsequent study is dependent entirely upon histological examination. These anomalies were noted in only a few of the sections taken from the oyster; sections taken more posteriorly were normal.

There are two possibilities as to the exact structure of these growths. These anomalies may represent cross sections through two discrete polyplike growths or cross sections through the end portions of a ridge-like growth. If the latter interpretation is correct, the ridged growth may have been 15 to 20 mm in length.

No attempt was made to classify these anomalies because of the lack of information concerning processes of abnormal growth in mollusks. These growths are not similar in size, location, or microscopic structure to those reported by other workers. Pauley (1967) stated that most of the tumors and other abnormal growths in mollusks were large and plainly visible externally. The tumorlike growths he described on the foot of freshwater mussels were visible externally, but were small (2 mm to 3 mm in diameter). The abnormalities described here were smaller and not visible externally. Microscopically, these growths were composed of relatively normal cellular elements in their normal anatomical locations. Lesions described by Smith (1934) and Sparks et al. (1964*a*) were composed of normal-appearing cells, but were in abnormal locations. The inflammatory response (leucocytic infiltration) in these growths is similar to that described by others and quite possibly is the result of repeated trauma.

FIGURE 3—The posterior growth in intestine of *Ostrea edulis*.

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FECUNDITY OF THE BROWN RAGFISH, *ICOSTEUS AENIGMATICUS* LOCKINGTON, FROM NORTHERN CALIFORNIA[1]

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During the period 1958–1963, five female brown ragfish were examined. With one possible exception, they had a few eggs running freely from the vent. Right ovaries from four specimens were studied in detail. Sizes and numbers of eggs were determined by taking 17 to 23 aliquot samples of ovarian tissue at different places along the length of the ovary. Three size categories of eggs were found in each ovary. Eggs in each category from ragfish taken in summer were smaller than those from fish taken during winter. A winter spawning is postulated. For eggs in the "large" category, a linear relationship existed between number of eggs and length of fish. This relationship, however, was based on data from only three specimens which presumably had not started to spawn before capture. The eggs of the species are not adhesive and so appear to be pelagic.

INTRODUCTION

The brown ragfish, *Icosteus aenigmaticus* Lockington 1880,[2] appears to be a deepwater fish. Its soft, white flesh makes it a poor food fish. Few specimens are landed and records are meager. Although through 1940 only three specimens had been reported from the waters off California (Bolin, 1940), these fish may be taken more frequently by commercial trawlers but returned to the sea. Of the five specimens made available to me, three were taken by a single trawling vessel, *City of Eureka*. The five ragfish in the present study were collected at the rate of about one per year over a 6-year span. In recent years, some specimens have found their way into collections but have not been reported in the literature. Abe (1954) reported on two juveniles from Japan, and the ichthyological collection of the Fisheries Department at Humboldt State College contains a juvenile specimen.

In the past, mainly morphological data have been presented in the literature. This paper is a study of the fecundity of the species based on ovaries from four of the five specimens (Table 1).

METHODS

Measurements

Total length, standard length, and maximum depth in centimeters were determined for four specimens, and weight in pounds for two specimens (Table 1). Total length was difficult to ascertain accurately because of the frayed caudal fin rays. The end of the hypural plate was

[1] Submitted for publication September 1967.
[2] The adult was first described as *Acrotus willoughbyi* by Bean (1887) (Clemens and Wilby, 1961).

TABLE 1

Information About Female Brown Ragfish Used in Fecundity Studies

Specimen number	Trawling vessel capturing specimen	Date of capture	Weight (pounds)	Length (cm)			Length of ovary in natural position	Ovary length as percentage of standard length	Depth (fathoms) and place of capture
				Total	Standard	Maximum depth			
1	*Sitka*	July 26, 1958	--	150	135	--	40.0	30	70; off Table Bluff, Eureka
2	*City of Eureka*	July 14, 1960	--	114	106	24	----	--	300; north Trinidad Head
3	*Rainbow*	Jan. 2, 1962	66	150	127	40	46.0	36	180–190; SW Humboldt Bay
4	*City of Eureka*	July 14, 1962	--	119	106	31	35.5	33	100; SW Humboldt Bay
5	*City of Eureka*	Nov. 19, 1963	51	129	124	37	39.0	31	230–240; off Mack Arch, Brookings, Oregon

located by external probing to measure standard length. Maximum body depth occurred slightly posterior to the gills.

Preservation and Description of Ovaries

After the specimens had been measured, their body cavities were opened and the dorsal and ventral mesenteries cut along the midline. The ovaries, bound together by mesentery and fascia, were slid gently into a deep pan and covered with formalin. Incisions were made in the heavy case surrounding the eggs and ovarian tissue to allow adequate penetration of fixative to all parts of the ovaries. Ovaries were retained in display jars until processed.

The ovaries are bilobed and occupy almost the entire body cavity. The ovaries themselves were about a third of the standard length of the fish (Table 1), and were of unequal length and shape. The right ovaries were longer and more slender than the left. Both ovaries were J-shaped posteriorly near the vent, but the right ovary more strongly so. On each ovary posteriorly, a complicated folding of mesentery forms oviduct channels that fuse into a common passage leading to the vent (Figure 1).

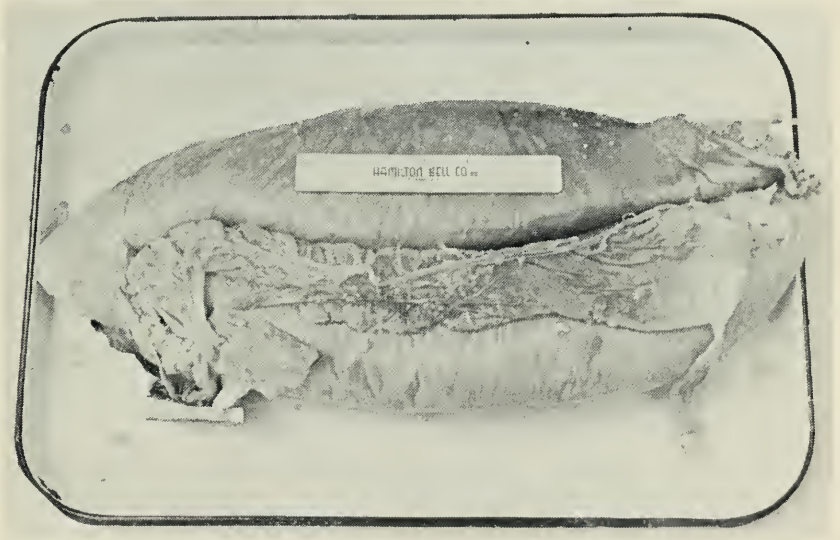

FIGURE 1—Ventral view of ovaries from brown ragfish, showing J-shape of right ovary located under 6-inch rule. (Pasterior is to left and anterior to right.)

Directly underlying the external mesentery tissue which surrounds the ovary, a thick layer of connective tissue forms what I term the ovarian case. The ovarian tissue with its developing eggs was only loosely attached to the ovarian case except dorsally near the midline, where it was strongly attached.

Procedures for Studying Eggs in Ovaries

Eggs were studied in the ovaries of four of the five specimens. The excepted specimen, delivered to Humboldt State College during the summer of 1960, was placed in a freezer and not processed until July 1962. The right gonad was badly ruptured and the left gonad slightly ruptured. In the remaining four specimens, only the right ovaries were studied, since they were the least damaged.

Depending on the size of the ovary, 17 to 23 aliquot samples were obtained from eight or nine predetermined positions along the length of the ovary. The number of aliquots taken from each position varied from one to three, with single aliquots being taken from the extreme ends of an ovary. Because of the J-shaped posterior end of the ovary, sections here most often yielded only one or two aliquots.

Aliquots were roughly 1 to 2 g of eggs plus ovarian tissue for specimens nos. 1, 4, and 5, and from 2 to 4 g for specimen no. 3. The water displacement in ml was also determined for aliquots. After eggs for each aliquot had been counted, the number of eggs (blotter-dried eggs plus ovarian tissue) per g and the number of eggs (water displaced eggs plus ovarian tissue) per ml were computed for all aliquots. Estimates of the number of eggs in the right ovary of each specimen were then made by multiplying the mean value of all aliquots from a specimen by the total volume in ml of water displaced by the right ovary, and by the 30-minuted drained total weight in g of the right ovary.

The first ovary to be studied was that of specimen no. 4. Aliquot samples of eggs plus ovarian tissue were taken in rapid succession. Since there were insufficient balances for weighing, a delay was encountered in processing samples. This introduced an error from differences in the degree of desiccation at time of weighing. This was remedied with the other specimens by keeping the 30-minute drained ovary moist under a wet cloth and only removing aliquots as balances became available. All samples were weighed immediately after removal from an ovary. This considerably reduced variability in results, as measured by the coefficient of variation (Table 2).

While human error could not be eliminated, the natural variability in the number of eggs per unit weight or volume of ovary greatly overshadowed any variation from this source.

Procedure for Obtaining Missing Data

In three specimens, the entire left ovary was weighed in the same manner as the right ovary. The left ovary of specimen no. 4 had been damaged so badly that this was not possible; therefore, I assumed that it weighed the same as the right ovary (Table 3). This assumption of equal weight between these ovaries appears to introduce only a slight error in estimating total eggs for this fish.

The ovarian case was weighed separately after removal from adhering eggs and ovarian tissue, and its weight ranged from about 5 to 10% of the remaining eggs plus ovarian tissue. The percentage weight of the ovarian case was assumed to be the same for both left and right ovaries in all specimens.

TABLE 2

Estimated Total Numbers of Large Eggs

Specimen number	Number of aliquots from right ovary	Number of eggs per gram of eggs plus ovarian tissue from aliquots of right ovary				Weight of eggs plus ovarian tissue of both ovaries (grams)	Estimated number of large eggs in both ovaries
		Mean	Range	Standard deviation	[1]Coef. var.		
1	23	261	156–335	38.2	15	1,647	430,000
3	18	79	64–94	7.2	9	2,911	230,000
4	17	296	201–457	71.8	24	989	293,000
5	20	124	98–153	11.5	9	3,163	392,000

[1] (Standard deviation/mean) × 100.

TABLE 3

Weights of Ovary Components * (Grams)

Specimen number	Right ovary			Left ovary		Eggs plus ovarian tissue		
	Entire	Case	$\frac{\text{Case}}{\text{Entire}} \times 100$	Entire	Case	Right ovary	Left ovary	Combined
1	927	88	9.60	894	(86)	839	(808)	1,647
3	1,488	71	4.79	1,569	(75)	1,417	(1,494)	2,911
4	541	48	8.87	(541)	(48)	493	(493)	989
5	1,564	85	5.12	1,775	(91)	1,479	(1,684)	3,163

* Missing data estimated by procedures explained in the text are shown in parentheses.

EGGS

Description

Clear, light-amber colored eggs, some of which were flowing freely from the vent, characterized all fish except specimen no. 2. Loose eggs were found in the body cavity, but there was no information on whether or not eggs were flowing freely from the vent of this fish in its fresh condition. At no time while handling these eggs did I notice any tendency for them to become sticky and adhere either to each other or to other objects. Thus, the eggs appear to be pelagic rather than demersal in character.

The approximate size of eggs was determined by measuring them with small plastic rulers calibrated in mm. In the first ovary to be studied (specimen no. 4), three categories of egg size were clearly discerned, but the measurements were not recorded. In the other ovaries, three size categories also were readily distinguished (Table 4). The degree of overlap between size categories was slight. Most overlap in size occurred between "large" and "medium" eggs from fish taken in July (specimens no. 1 and 4), and between medium and "small" eggs from specimens taken in November and January (specimens no. 5 and 3). In three specimens, there were relatively few eggs in the medium category; however, in specimen no. 5 there were about equal numbers of large and medium eggs (Table 5).

TABLE 4

Sizes of Eggs in Ovaries

Specimen number	Month of capture	Category, and size of eggs (millimeters)			Degree of overlap between categories
		Large	Medium	Small	
1	July	1.5–1.0	0.75–0.5	<0.1	Some between large and medium
4	July (not available)	----	----	----	Some between large and medium
5	November	3.0–2.0	1.0–0.5	<0.5	None reported
3	January	3.0–2.5	2.5–1.0	<1.0	Some between medium and small

TABLE 5

Relative Numbers of Large and Medium Eggs

Specimen number	Number of eggs		Ratio of large to medium eggs	Number of aliquots counted
	Large	Medium		
4	2,166	129	17:1	5
5	4,058	4,122	0.9:1	19
3	3,123	175	19:1	15

Number

The number of large-category eggs was counted in all aliquots taken from the right ovaries of the specimens studied. The mean number of eggs per g was used to convert the estimated weight of both ovaries to total estimated number of eggs for each specimen. The number of large-category eggs ranged from 230,000 to 430,000 (Table 2).

The relationship of eggs in the large category to their position within the ovary was investigated. The numbers of eggs per g calculated for each aliquot sample were plotted on an outline of the ovary by place of sampling. In all specimens, no pattern of egg size in relation to position in the ovary could be discerned. Frequently, extreme values found in any one ovary lay at adjacent sampling sites. Our data indicated that eggs in the large category were developing simultaneously at all points within the ovary.

TIME OF SPAWNING

As mentioned previously, eggs were found freely flowing from four of the ragfish studied. I observed two of these specimens when they were relatively fresh from the sea. Although the actual number of eggs flowing from the vent was very small in comparison with the eggs in the ovaries, the eggs appeared ready for extrusion under natural conditions. An increase in the size of eggs in all categories with progression from summer to winter indicates a process of maturation with egg extrusion in the winter (Table 4). A winter spawning is also in-

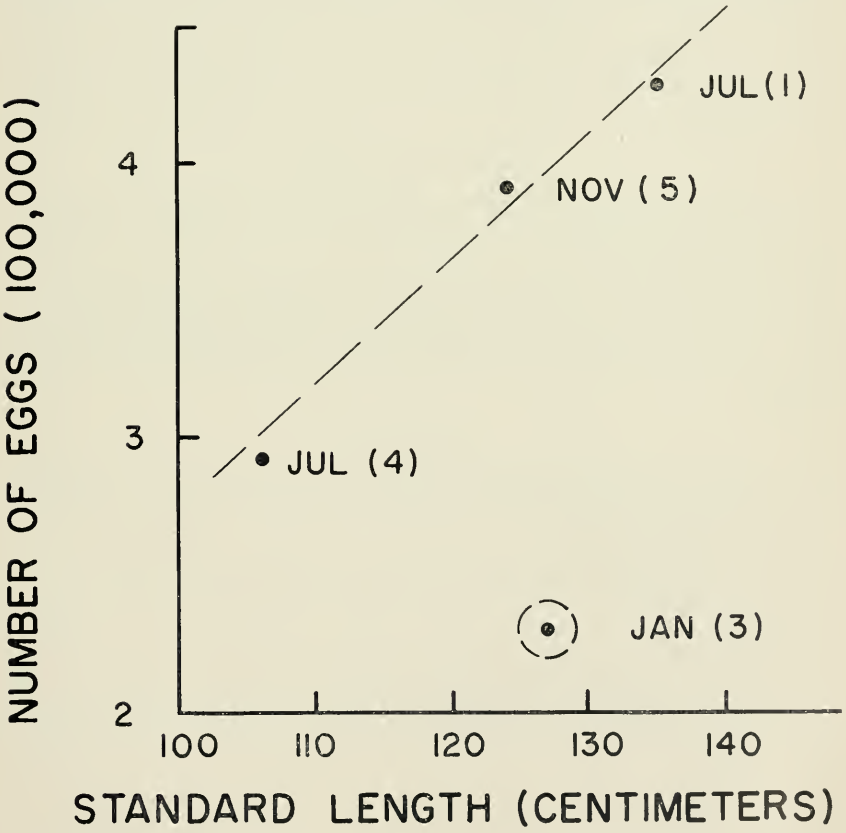

FIGURE 2—Relationship between total estimated number of large-category eggs and standard length of four brown ragfish from the Pacific Ocean off northern California (specimen numbers in parentheses).

dicated when the total number of eggs is plotted against length of fish by month of capture (Figure 2). Three of the four specimens show a linear relationship between size of fish and number of large-category eggs (Figure 2). The fourth fish (specimen no. 3, captured in January) had fewer eggs for its length than the other specimens. Possibly this specimen was caught during the process of spawning and therefore contained fewer large-category eggs for its length than the other specimens, which were taken presumably before spawning. Moreover, the egg sizes in all categories were the largest for the fish taken in January (specimen no. 3).

While the relatively large number of eggs found in the medium category for specimen no. 5 (Table 5) and the overlap between categories changing with season of the year (Table 4) are confusing, it is possible that the method of study produced an artifact, and that only two sizes of eggs may have existed.

FECUNDITY

No data are available at this time as to how long eggs of the sizes found in the specimen studied are retained before extrusion, or whether spawning is restricted in time or is a continuous process. Thus, fecundity defined as the number of eggs produced by a fish during a year cannot be stated with certainty. Nevertheless, if a single ragfish spawning per year does occur, as suggested by the present data, the number of eggs found in the three specimens taken in July and September must be considered.

ACKNOWLEDGMENTS

Commercial fisheries students at Humboldt State College assisted in the study of the size and number of eggs in ovaries. These efforts are gratefully acknowledged.

I also wish to express appreciation to commercial fishermen who retained specimens of ragfish, especially Dick Young, John Kinder, and Nick Picola. Paul Reed and Glen Brackett, California Department of Fish and Game, assisted in transporting specimens to Humboldt State College.

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NOTES

THE 1967 SHARK KILL IN SAN FRANCISCO BAY

Mass mortality of fishes has occurred in San Francisco Bay a number of times in the past. The last major kill happened in 1957, when great numbers of large striped bass were found strewn along several miles of the east side of the bay. That disaster was caused by a toxic chemical effluent, and the manufacturing company responsible for the effluent was fined for violating state laws. Unfortunately, such a clear-cut source of contamination cannot always be pinpointed. During July and August 1967, more than 725 elasmobranchs of four species were affected along the western shores of Alameda by an unknown contaminant.

During the first part of July, there were many reports of small sharks being washed ashore on the Oakland side of the bay, particularly along the Alameda Beach Regional Recreation Area. This shoreline is about $1\frac{1}{2}$ miles in length and is approximately due east of Golden Gate Park in San Francisco. We made repeated observations, but did not keep detailed counts until July 31. Based on these counts, we estimate that at least 200 sharks were washed ashore between July 15 and 30. Most of these were leopard sharks, *Triakis semifasciata*. Later, leopards seemed to be less common.

The aberrant swimming behavior of poisoned brown smoothhound sharks, *Rhinotriacis henlei,* was observed on several occasions. They swam quite irregularly—to the point of crashing into shoreline rocks and trying to move over them, coming out of the water sometimes as much as half the length of their bodies. In water 3 ft deep, a number of sharks were observed swimming at the surface with the dorsal fin protruding. Several live sharks that had just beached themselves were thrown back into the water, where they resumed swimming only to return to the shore in 5 or 10 minutes. They seemed to be quite insensitive to objects in their paths. Almost a dozen sharks were observed swimming in a circular fashion, but these eventually beached themselves.

One 7-ft sevengill shark, *Notorynchus maculatus*, was found, as well as one striped bass, *Roccus saxatilis*, weighing about 10 pounds. The relative absence of striped bass seemed to indicate a different type of toxic material than that responsible for earlier kills. Although birds were observed feeding on the sharks, we encountered only one dead seagull.

Beginning July 31, daily counts were made by Don Wilson (Naturalist-preparator, East Bay Regional Park District). Each shark was marked and removed from the area so it would not be counted a second time. Between July 31 and August 10, 338 elasmobranchs were counted, including 330 brown smoothhounds (67 males and 263 females), 4 female leopards, and 4 female bat stingrays, *Mylicbatis californicus*. This was an average of 30 elasmobranchs per day; however, during the next

22 days (August 11 to September 1) the average was only eight and one-fourth per day. In this period, a total of 183 animals was counted: 162 brown smoothhounds (22 males and 140 females), 8 leopards (3 males and 5 females), and 13 bat stingrays (3 males and 10 females).

The brown smoothhounds were the most abundant, with 492 recorded mortalities during the 33-day counting period (July 31 to September 1). Of this number, 18% (89) were males and 82% (403) were females. This ratio (1 male to 4.5 females) approximates the normal sex ratio of about 1:3 for San Francisco Bay brown smoothhounds. For leopards and bat stingrays the normal San Francisco Bay ratio is about 1:1.

From the species of sharks that apparently were not affected we can deduce something about the toxic material responsible for this mass mortality. Dogfish, *Squalus acanthias*, and soupfin, *Galeorhinus zyopterus*, are reasonably common in San Francisco Bay, with each representing about 10% of the total bay elasmobranch population. Both species are fast-swimming sharks that seldom come to the bottom. With the exception of the sevengill, all of those killed (brown smoothhound, leopard, and bat stingray) are typical bottom forms. The smoothhound and bat stingray spend more than 75% of their time sitting on the bottom or foraging just above the bottom, while the leopard spends about 25% of its time on the bottom. Consequently, this toxic material must have been something which spread out over the bottom of the bay for a considerable area and had a breakdown period that lasted more than 2 months.

We were unable to localize the source of the contamination. The only major observable difference in the area just before the mortalities was the presence of large aircraft carriers in dock at the Alameda Naval Air Station, located just north of the beach area where the sharks were collected. Whether untreated effluents either from repair work or from normal activities aboard these ships could have contained toxic materials was not determined.

—*Ronald A. Russo and Earl S. Herald, East Bay Regional Park District, Oakland, California, and Steinhart Aquarium, California Academy of Sciences, San Francisco, California, February 1968.*

NORTHERN RANGE EXTENSION FOR THE KELP BASS, *PARALABRAX CLATHRATUS* (GIRARD)

A kelp bass captured near the entrance of the Columbia River extends the known range of this species some 345 miles northward. The previously reported northernmost limit was Trinidad Head, Humboldt County, California (Smith and Gotshall, 1967).

On September 11, 1965, a male kelp bass, 34.8 cm TL, was caught by a fisherman on the sport fishing boat *Dreamer*, operating out of Hendrickson's Moorage, Warrenton, Oregon. The specimen was taken while trolling for salmon at approximately 46°14′N lat, 124°06′W long, 1 mile south of the entrance of the Columbia River. Recognized as unusual for the area, it was positively identified as *Paralabrax clathratus* by the junior author and is now in the ichthyological collection of the

Department of Fisheries and Wildlife, Oregon State University, accession number OS 2397.

Scales from the fish had six annuli, which indicates a rate of growth comparable to kelp bass from southern California (Young, 1963).

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—*Michael J. Hosie and Carl E. Bond, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, February 1968.*

NORTHERN RANGE EXTENSION FOR THE YELLOW CRAB, *CANCER ANTHONYI*

Six yellow crabs, *Cancer anthonyi,* were taken in Humboldt Bay by Department of Fish and Game personnel between December 1964 and May 1967. The first, a male with a carapace width of 124 mm, was taken on December 12, 1964, in a trap. The second, another male (106-mm carapace width), was taken on January 12, 1967, during otter trawl operations. The third, a female (84-mm carapace width), was taken in a trap February 8, 1967. Two males and a female, 100-mm, 113-mm, and 90-mm carapace width, respectively, were taken in traps during May 1967.

The reported northern range limit of this species was Monterey Bay (Phillips, 1939). The yellow crab has been observed by Department of Fish and Game personnel in trapping and trawling operations in the San Francisco and Bodega Bay areas since the late 1950's. The six specimens taken in Humboldt Bay extend the range northward by 275 miles.

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Phillips, J. B. 1939. The market crab of California and its close relatives. Calif. Fish and Game. 25(1) : 18–29.

—*Mel Willis, Marine Resources Operations, California Department of Fish and Game, November 1967.*

BOOK REVIEWS

Sharks, Skates, and Rays

Edited by Perry W. Gilbert, Robert F. Mathewson, and David P. Rall; The Johns Hopkins Press, Baltimore, 1967; xvi + 624 p., illustrated. $15.

Sharks, skates, and rays is a collection of 39 papers that were presented during a 6-day symposium at Bimini, Bahamas, in 1966 entitled, "Current investigations dealing with elasmobranch biology." This book has been divided into five parts: (i) Phylogeny, taxonomy, and distribution; (ii) Osmoregulation, salt and water metabolism; (iii) Dentition; (iv) Central nervous system and special senses; and (v) Pharmacology, endocrinology, and immunology; and each of these contains the contributions pertaining to it.

Part 1 (172 pages) comprises nine papers, and perhaps the best way to illustrate their diversity is to list these by title and author: (i) Comments on elasmobranch evolution (Bobb Schaeffer); (ii) A survey of shark hard parts (Shelton P. Applegate); (iii) A taxonomic synopsis of the hammerhead sharks (Family Sphyrnidae) (Carter R. Gilbert); (iv) Observations on the hammerhead sharks (*Sphyrna*) in waters near Mazatlan, Sinaloa, Mexico (Anatolio H. Carvallo); (v) A broad view of *Carcharhinus* species, their systematics and distribution (J. A. F. Garrick); (vi) Shark tagging in the eastern Pacific Ocean, 1962–65 (Susumu Kato and A. H. Carvallo); (vii) Tag evaluation and shark tagging in South African waters, 1964–65 (David H. Davies and L. S. Joubert); (viii) Depth segregations and distribution of sex-maturity groups in the marbled catshark, *Galeus arae* (Harvey R. Bullis, Jr.); and (ix) Social organization of shark populations (Stewart Springer).

Both Carter Gilbert and Anatolio Carvallo present keys to the hammerheads in their respective papers, and Gilbert has an almost identical key in his 1967 publication entitled "A revision of the hammerhead sharks (Family Sphyrnidae)." (Proc. U.S. Natl. Mus., 119:1–88). The principal difference in Gilbert's two keys is the exclusion of *S. couardi* in the 1967 publication on the grounds of not having seen a whole specimen. Anatolio Carvallo lists five species for the Mazatlan area: *zygaena*, *tiburo* (= *tiburo vespertina* of Gilbert), *mokarran*, *media*, and *lewini*. He discusses abundance, distribution, and similar details for each of these.

Although many of the contributions can be read and understood by individuals with only slight scientific background, the book will have its greatest appeal among professional ichthyologists and fishery biologists. Its potential usefulness in a reference library should justify the purchase of more than one copy, particularly by high schools, colleges, and universities.—*John E. Fitch.*

Proceedings of the Symposium on the Biology of the California Islands

Edited by Ralph N. Philbrick; Santa Barbara Botanic Garden, Santa Barbara, Calif., 1967; 363 p., illustrated. $10.

Between Point Conception, California, and Punta Eugenia, Baja California, lie 16 major islands, eight off the coast of southern California and eight off Baja California; these are the "California Islands" treated in this book. The symposium, a 2-day affair sponsored by the Santa Barbara Botanic Garden, was held October 29 and 30, 1965; the collection of 19 formal manuscripts presented at this symposium, with a foreword and introduction, and interspersed with discussions, comprise this 363-page volume.

Such general subjects as Cenozoic history, flora, fauna, geochronology, and archaeology are covered—some lightly and others extremely well. Helpful tabular information includes data on total land area and distance from the mainland for each island. An index of scientific names is extremely helpful and seems to be quite complete.

Search as I might, I could find no mention of the California Department of Fish and Game in a chapter by John B. Loefer, Office of Naval Research, Pasadena, entitled "Institutional scientific interests in the southern California Islands." Mentioned were more than a dozen educational and research institutions (both

public and private), marine laboratories, governmental agencies, etc., etc., but no place could I find reference to the one agency which historically has had and continues to have a greater vested interest in the flora and fauna living on and around these islands than perhaps all the other institutions combined. Fortunately, most of the other contributors were more knowledgeable in their presentations, but few of the accounts are intended to represent exhaustive studies or the final word.

Generally, this collection of contributions combines the theories and findings of numerous individuals, who have devoted many years of their lives researching the paleontology, geology, biology, and archaeology of the islands. The contents of the various chapters should prove especially helpful to those who are involved in similar studies but also will provide useful information and interesting reading to those with only a passing concern.—*John E. Fitch.*

Fish Cookery

By J. Charles Davis, 2nd; A. S. Barnes and Co., Inc., Cranbury, New Jersey, 1967; 226 p. $5.95.

Noted sport fisherman and author J. Charles Davis, 2nd, is convinced that many people acquire a dislike for fish merely because they have never learned to prepare this kind of food properly. Disturbed by such an unwarranted prejudice and certain that anyone can learn to cook fish successfully, he has published his extensive collection of fish recipes in a book appropriately entitled "Fish Cookery".

The author first disposes of the question, "Why eat fish?", by quoting from a fish cookbook published in 1933 by the (then) California Division of Fish and Game. Although this publication has been out of print for many years, the facts regarding the food value of fish are still valid. Likewise, some of the outstanding recipes in the Division's cookbook have been rescued from obscurity by Mr. Davis. These and many more interesting and unique recipes are offered for the guidance of the reader in preparing a variety of marine and freshwater fishes for the table. The author also includes instructions for cooking such delicacies as shellfish, turtles, frogs, and whale.

Supplementing the recipes are chapters presenting practical cooking tips, definitions of cooking terms, and a discussion of the types of cooking utensils that will produce the best results. Unfortunately, the illustrations referred to in the chapter on filleting and skinning fish were omitted. These would have been of value in describing processes which require considerable skill.

Throughout the 226 pages of this book, the author's salty language supplies a special flavor to an otherwise bland subject. Anyone interested in cooking will enjoy this book, but it will have a special appeal to the angler who wants his catch served in the most appetizing manner. —*George H. Warner.*

The Campers' Cookbook

By Lucy G. Raup; Charles E. Tuttle Co., Inc., Rutland, Vermont, 1967; 199 p. $3.

Cookbooks generally contain little more than a collection of recipes and cooking instructions. *The Campers' Cookbook* differs from this pattern, although author Lucy G. Raup does provide the camp cook with a choice of more than 200 easy-to-follow recipes. The significant feature of this book is that it tells campers how to get ready to cook. Packing provisions, setting up camp kitchens, selecting firewood, and building cooking fires are some of the camping skills explained in the text. For either the novice or experienced camper, Raup's basic ration list will be of value in menu planning. This list may be adjusted for any type of camping from a backpack trip to a vacation at a permanent camp site where weight and bulk of supplies are not important. Through the use of symbols, information applicable to various kinds of camping is identified throughout the book.

The importance of planning a cooking schedule so that all parts of the meal will be ready at the same time is stressed and time tables for cooking have been included for this purpose. Unfortunately, the effect of altitude on cooking time is not mentioned. In spite of this oversight and the fact that the author advocates burying garbage instead of burning it in the approved Boy Scout manner, campers will find this cookbook to be well worth its modest price.—*George H. Warner.*

Modern ABC's of Bow and Arrow

By G. Howard Gillelan; Stackpole Books, Harrisburg, Pa., 1967; 160 p., illustroted. $4.95.

G. Howard Gillelan, archery editor for *Outdoor Life*, has produced another in a series of popular books published by Stackpole Books presenting the basic fundamentals of outdoor sports.

This informative little book equips both the beginner and experienced archer with the know-how of archery. It gives the fundamentals of target and field archery and tips on bowhunting. Most important, the chapters "What to Buy and Why", "What is the Best Bow for You", "It's a Matter of Form", and "Does it Pay to Make Your Own Gear" answer the many basic questions posed by those interested in archery.

Modern ABC's of Bow and Arrow is highly recommended reading for the newcomer and an excellent reference text for the experienced archer.—*Howard R. Leach.*

Be Expert With Map and Compass (The "Orienteering" Handbook: New Revised Edition)

By Bjorn Kjellstrom; Stackpole Books, Harrisburg, Pa., 1967; 136 p. + mop, profusely illustrated. $3.95.

Systems Analysis in Ecology

Edited by Kenneth E. F. Watt, Academic Press, New York and London, 1966; ix + 276 p., illustrated. $11.50.

In the editor's words, "This book is designed to survey the problems and techniques of systems analysis in ecology." It presents a stimulating exposition of the need for systems analysis in ecological studies and serves as an introduction to this field. The book is a compilation of nine essentially independent articles by different authors tied together by an introductory chapter on systems analysis by the editor.

Individual chapters include a general discussion of ecological systems to illustrate their complexity and the management problems this poses; a description of a large ecological systems study to illustrate the methods and problems involved; three articles dealing with the measurement of animal behavior using automated monitoring devices; an interesting paper dealing largely with one small phase of statistical analysis; an article on modelling behavioral processes; an article on modelling complex systems as a whole; and a discussion of the future in ecology.

As so often happens in such a group effort, the book suffers some from a lack of unity, and some papers include minutiae not essential to the general purpose of the volume. I also would have preferred to see less emphasis on measurement techniques and more emphasis on modelling. I had hoped to gain a better understanding than I did of the present utility of modelling for solving management problems.

On the whole, though, the book presents many stimulating ideas. I strongly recommend that all biologists read it and consider its implications for the future of resource management.—*Harold K. Chadwick.*

The Life of the Ocean

By N. J. Berrill; McGraw-Hill Book Co., New York, 1966, 232 p., illustrated with 117 color photographs and over 100 diagrams, maps, and sketches. $4.95.

The Life of the Ocean is a skillful and artful blending of lively text, brilliant color photographs, and informative sketches of plants and animals associated with the marine environment. The book's style and format, a cross between a slick magazine and the World Book Encyclopedia (cooperators), is obviously meant for the general interest reader. This book is also one of a series titled *Our Living World of Nature.*

The spectacular, eye catching, story telling photographs tend to mask out the eloquent and information-packed narration by Dr. Berrill. His lucid prose is equally fitting in describing the plants and animals as well as the dynamic, interacting processes of the ecosystem in which they dwell. Interwoven throughout the text are historical, scientific, and statistical facts which enliven and heighten reader interest. The oceanographic disciplines of botany, zoology, geology, hydrology, meteorology, chemistry, and physics, plus some of man's modifying activities, are skillfully synthesized by Dr. Berrill in his story of life in the oceans.

For the reader who wishes to delve deeper there is an appendix containing the following sections: "Ocean Life and Our National Parks"; "Endangered Ocean Animals"; "Sharks"; "Mammals of the Ocean"; "Man in the Ocean"; "Keeping Ocean Animals in the Home"; "A Walk Along the Shore"; plus a glossary and a short but excellent bibliography.

One glaring omission seriously detracts from the book's intended use. The appendix contains two sections which depict, with sketches and short paragraphs, representatives of the "Sharks and Their Relatives" and "Mammals of the Ocean". The significant teleosts, or bony fishes, are completely ignored!

The book also suffers from being a bit too "arty". Any number of interesting, indeed exceptional, photographs lose their impact by being printed across two facing pages, where their continuity is disrupted by the dip at the binding. The viperfish, pages 98–99; the underwater shot of elkhorn coral, pages 146–147; and the diagram of plankton migrations, pages 88–89, are typical examples.

In an era of rising prices, wherein books are no exception, it is indeed a wonder that a book of this scope and quality can be offered to the public for the nominal price of $4.95.—*Leo Pinkas.*

Advances in Ecological Research, Volume 4

Edited by J B. Cragg, Academic Press, London and New York, 1967; xi + 311 p., illustrated. 80s. $13.50.

Editor Cragg has again assembled a stimulating and useful set of papers in an attractive volume. Dr. Richard Miller of the University of Saskatchewan writes a lucid and well-documented account of "Patterns and Processes in Competition" in which he explores the question "How does competition really work?" Dr. N. W. Moore of Nature Conservancy's Monks Wood Experimental Station, England, contributes "A Synopsis of the Pesticide Problem", Dr. Bernard Stonehouse, Canterbury University, Christ Church, New Zealand, writes of "The General Biology and Thermal Balances of Penguins". The fourth and last paper, by Professor J. A. Kitching and Dr. F. J. Ebling, is "Ecological Studies at Lough Ine", an interesting account of a great deal of work to find out what controls the distribution and abundance of marine organisms in an Irish lake of seawater and the tidal "rapids" that connect it with the sea.—*D. W. Kelley.*

The Avalanche Enigma

By Colin Fraser; Rand McNally & Co., Chicago, 1966; xvi + 301 p., illustrated. $6.95.

Most of the books written about avalanches are of a highly technical nature and are not of interest to the general reading public. This well-written and informative book by Colin Fraser is far different. Any person with some interest in the mountains and the workings of nature will be captured by his writing.

The author discusses avalanches—from the earliest recorded in history to the present time—including the reasons for them, modern research, and the latest in avalanche predictions and preventions, including numerous personal experiences. The work contains 49 photographs and 14 drawings of interest.

The descriptions of the various types of snow, their buildup, and their release in the various avalanche forms is written in such interesting manner, with numerous factual incidents, that the reader's interest is increased as he proceeds in the book. Mr. Fraser is well qualified to write of avalanches because of the knowledge and experience he has accumulated in many years of living in Switzerland and research with the Swiss rescue teams and avalanche research centers.

I think that this book will be enjoyed by any person whoever goes into the mountains, winter or summer. The increased knowledge it imparts can be used by any person who travels in these areas.—*Hugh L. Thomas.*

In Wildness Is the Preservation of the World

Text selections from Henry David Thoreau and color photographs by Eliot Porter; Sierra Club-Ballantine Books, Inc., New York, N. Y., 1967, 160 p. $3.95 (paper).

This paperback version of the popular hardback edition is smaller in size and price but suffers little in quality in comparison with its larger counterpart.

In the Introduction conservationist Joseph Wood Kritch commends Eliot Porter for his brilliant artistic photography. ". . . he has realized that the way to add to

what Thoreau has written was to catch Thoreau's spirit, to see with his eye the kind of thing he saw and loved. As a result Porter's pictures are truly in the spirit of Thoreau."

The color of these photographs is brilliant. The excellent passages from Thoreau have been meticulously selected from the whole of his works. Thoreau's concern for nature over a century ago is perhaps even more appropriate in our time.

This anthology and its outstanding photography must be read and seen to be fully appreciated. This book is a must for the nature lover, conservationist, and photographer.—*Lee W. Miller.*

The Biology of the Striped Skunk

By B. J. Verts; University of Illinois Press, Urbana, 1967; xiv + 218 p., illustrated. $7.95.

This book is a comprehensive publication on the life history of the striped skunk in Illinois. The original objective of this study was to "determine the prevalence and degree of interspecific transmission of rabies among various species of carnivorous and insectivorous mammals". Because of the reported incidence of rabies among striped skunks in the Midwestern United States, exceeding by several times the incidence in other mammals, the emphasis of the study centered on the skunk and its role in the epizootiology of the disease. The primary objective became a comprehensive life history study of the striped skunk and relation of the knowledge obtained to the frequency of rabies in the northwest Illinois skunk population.

The author made a complete review of the available literature and with approximately 5½ years of basic field data, observations, and trapping information put together an excellent publication on the life history of one of our more common mammals. Eleven chapters provide detailed information on the history of the striped skunk, external morphology, growth behavior, reproduction, food habits, population dynamics, and diseases. One chapter is devoted to rabies, covering the subject from the early history and distribution of the disease to the behavior of infected animals.

A complete and concise review of available information, coupled with the author's own experiences and data, provide us with an important reference book. Information contained in this book will be of great assistance in the understanding and management of this species.—*Robert D. Mallette.*

Development of Fishes of the Chesapeake Bay Region: An Atlas of Egg, Larval, and Juvenile Stages. Part I.

By Alice J. Mansueti and Jerry D. Hardy, Jr., Natural Resources Institute, University of Maryland, Salomons, Maryland, 1967; 6 + 202 p., 90 figures. $9.50.

This book will be welcomed by anyone who has struggled to identify unknown fish eggs and larvae.

In writing this atlas the authors have carried on the work of the late Dr. Romeo Mansueti. It was his concept to bring together into one reference all the knowledge about Chesapeake Bay fish eggs and larvae which was unpublished or scattered through the literature.

In Part I of the Atlas, 45 species of the following fish are included: sturgeon, gar, bowfin, tarpons, bonefish, herring, anchovies, mudminnow, pikes, lizardfishes, minnows and carps, suckers, sea catfishes, and catfishes. A species is included if any of its life history stages occurs in Chesapeake Bay or its tributaries, or in estuarine and coastal waters of New Jersey, Delaware, Maryland, and Virginia. Some of the freshwater and anadromous species are also found in California. Eventually the Atlas will include 230 species of fishes.

A complete, concise description of the eggs, yolk-sac larvae, larvae, prejuveniles, and juveniles of each species is presented and profusely illustrated. In addition, there is an illustration and description of the adult, along with sections on distribution, ecology, and spawning requirements for each species.

The list of approximately 900 titles in the bibliography will be invaluable to anyone conducting a literature search on the subject of fish eggs and larvae.—*Timothy C. Farley.*

Estuaries

Edited by George H. Lauff; American Association for the Advancement of Science, Washington, D.C., 1967; xv + 757 p., illustrated. $27.

The papers presented at the Conference on Estuaries held at Jekyll Island, Georgia, in 1964 are published in this volume. It includes 71 papers grouped into the following 10 categories: basic considerations, physical factors, geomorphology, sediments and sedimentation, microbiota, nutrients and biological production, ecology and population, physiology and evolution, fisheries, and human influences.

As this list indicates, the book attempts to cover virtually all aspects of estuarine ecology, and indeed it accomplishes this objective very well. The only major omissions I noted are that little is included on shellfish or on aspects of tidal hydraulics other than circulation and diffusion. Many seldom considered subjects, such as the available knowledge on the roles of fungi, yeasts, and detritus, are well covered. Also, there is surprisingly little repetition, considering that the papers are independent of each other.

Types of subjects of individual papers range from quite detailed discussions of either methodology or specific studies to extensive monographs. The latter make the volume particularly valuable.

The volume's value is also enhanced by the extensive bibliographies included for many papers and by a supplemental bibliography of papers published after 1964.

A few of the papers are so general and offer so little supporting evidence that they are of little value, and a few give the impression of having been written hastily. However, on the whole those who organized the conference, participated in it, and prepared this volume did an excellent job and performed a valuable service. I heartily recommend this book to all those participating in ecological studies of estuaries or concerned with estuarine management.—*Harold K. Chadwick.*

Symbiosis. Volume 1. Associations of Microorganisms, Plants, and Marine Organisms

Symbiosis. Volume 2. Associations of Invertebrates, Birds, Ruminants, and Other Biota

Edited by S. Mark Henry; Academic Press, New York, 1966 and 1967; xviii + 478 p., illustrated, and xv + 443 p., illustrated. $16.50 and $17.50.

Webster's New International Dictionary (Second Edition) defines symbiosis as: "The living together in more or less intimate association or even close union of two dissimilar organisms." The editor of these two volumes defines symbiosis simply as the "living-together of two or more species". According to the editor, the intent of this review of symbiosis was to bring together as much of the knowledge of the subject as possible, stressing the "interspecific cooperation".

Unfortunately, as pointed out in the preface, some of the authors did not follow the guidelines and put too much stress on parasitism.

The first volume covers mutualistic, commensal, and parasitic relationships between microbes, including bacteria, fungi, algae, protozoa, and viruses; algae and fungi (= lichens); bacteria and plants; fungi and plants; algae and invertebrates; and marine invertebrates. The last two chapters are devoted to a review of marine cleaning symbiosis, and studies of behavior and symbiosis. Insects, birds, and mammal associations are covered in the second volume; the bulk of the papers deal with insect symbiosis.

I particularly was interested in and enjoyed the chapter on marine invertebrate symbiosis, and cleaning symbiosis. The cleaning symbiosis paper probably contains the most up-to-date (through 1964) collection of knowledge on this subject, and should serve as a valuable reference and bibliography in any future studies. The author of this paper lists a total of 63 references on the subject.

I would not recommend these volumes for the casual reader in biology, unless he is willing to spend many hours in learning the vocabularies of the various specialties involved. However, the two volumes should prove to be an excellent reference for researchers and educators in the fields of marine biology, entomology, ornithology, mammalogy, plant physiology, and biochemistry. They could also be used as texts in a specialized course on symbiosis.—*Daniel W. Gotshall.*

The Trout

By W. E. Frost and M. E. Brown; Collins, London, 1967; 286 p., illustrated. $5.

This is another of The New Naturalist Special Volumes designed to stimulate the general reader's interest in the wildlife of Britain and concern for its conservation. This is accomplished, ". . . by maintaining a high standard of accuracy combined with clarity of exposition in presenting the results of modern scientific research." The authors have accomplished this goal, although the book may be somewhat technical for the general reader. However, it certainly wouldn't be for the intelligent and curious layman, and it is from their ranks that conservation draws its most influential and industrious supporters. Without doubt, fishery students and professional fishery scientists also will benefit from and thoroughly enjoy *The Trout*.

The authors are prominent British scientists (both women by the way) who combined their great knowledge and experience to produce this excellent little monograph on the brown trout, *Salmo trutta*. This, plus the blend of their two specialties, assured success. Dr. Frost is noted for her investigations of the fish and fish foods of River Liffey in Ireland and Lake Windermere in Britain, while Dr. Brown is renowned for studies of salmonid physiology and was the editor of the classic two-volume *Physiology of Fishes*.

Illustrations are plentiful and extremely well done, particularly the photographs, 4 in color and 42 in black and white. The color photos are actually a single plate comprising a montage of four pictures of different color phases of the brown trout. I observed what appeared to be these same types and possibly others at Lake Tahoe. As always, photos of the scenic surroundings of British and Irish lakes and streams are a pleasure to behold. Excellent detail can be found in a series of 12 pictures of brown trout scales and 5 showing spawning brown trout.

The authors have virtually ignored studies conducted in the United States, although they commonly refer to work done outside the British Isles in Kenya, New Zealand, Tasmania, Europe, and Canada. This shortcoming is particularly apparent in the chapter "Trout and Man". Citation of studies conducted in the U. S. on brown trout population dynamics and experimental stocking programs would have substantially strengthened this chapter. Omission of or lack of familiarity with such literature may be responsible for occasional puzzling statements such as, "Brown trout are stocked in many waters in Canada and U. S. A. but, on the whole, they do not spawn successfully and are less esteemed by anglers than the excellent native 'trouts' . . ." Also, they mention that ". . . there is sound evidence for a 'homing instinct' in trout . . . The means whereby the trout find their way back to their own stream is not yet established." Hasler's important work on odor perception goes unmentioned.

Any shortcomings are minor compared with the book's merits, however. There are chapters on Anatomy and Physiology, Taxonomy, Distribution, Life History, Age and Growth, Heredity, The Physical Environment, The Trout's Food, The Biological Environment, and Trout and Man. Methods of making standard age and growth determinations and calculating specific growth rates are among the eight appendices. An impressive list of references and an excellent subject index round out the treatise. It is certain that the literature on freshwater fishes could well use more high quality monographs such as this.—*Almo J. Cordone.*

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